

COOPERATION AND CONFLICT:
SOCIALITY IN SALTICID SPIDERS

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ABSTRACT

By studying salticid spiders from East Africa I look at sociality from an unusual perspective. These particular salticids form mixed-species groups, with more than one species and even more than one genus routinely living together within any single nest complex. The primary occupants of these nest complexes are three species of *Menemerus*, two species of *Pseudicius*, *Myrmarachne melanotarsa* (Wesolowska and Salm, 2002), *Parajotus cinereus* (Wesolowska, 2004), and an unidentified species that I call the ‘Nun’. Adult males and females, along with juveniles of different age classes, share nest complexes. The highly varied composition of these groups suggests that the benefits to the salticids of grouping extend beyond species boundaries. Relatedness may not be so critical for understanding the dynamics of these inter-spider relationships. This suggests a departure from how social spiders have been studied in the past.

Often *Portia africana* (Simon, 1886) is also a part of the nest-complex community. Although solitary as an adult, *P. africana* has a social juvenile phase, and juveniles of *P. africana* sometimes even share prey. The cues that *P. africana* use when making decisions to join others and cooperate in prey ambush suggests at least rudimentary numerical ability in these spiders. *Myrmarachne melanotarsa*, a new species described during this study, is a myrmecomorphic salticid that lives in close proximity to the ant it mimics, a species of *Crematogaster*. Links between the biology of the ant the ant mimic are investigated. Access to honeydew and defense by collective mimicry appear to be unusual, but especially important, aspects of this species’ biology. *M. melanotarsa* is also routinely found living close to other salticid species, and it has a preference for juveniles of other salticids as prey. Clustering with reproductive groups of other salticids appears to be important as a means by which *M. melanotarsa* gains access to this unusual prey.

Yet another social salticid species, *Menemerus* sp. A, has a special relationship with ants. It steals prey from foraging ants. Besides ants, two assassin-bug species (Reduviidae), *Scipinnia*

repax and *Nagusta* sp., associate with the social salticids. Both feed by preference on salticids. *S. repax* also singles out *Nagusta* sp. as prey. For the salticids, one advantage of living in nest complexes appear to be that the large silk edifice a group of salticids may build provides partial protection from predators such as ants and reduviids.

Experiments show that social salticid species actively choose to group with other conspecifics and with social salticids from other species and genera. However, aside from *M. melanotarsa*, all of the social salticid species are averse to joining nest complexes containing ants.

The adaptive significance of the array of different relationships and interactions within the nest complexes is discussed.

Chapter 1

Introduction

Attempts at specifying the meaning of ‘social’, ‘sociality’, ‘society’ and related terms have met with minimal success, partly because biological attributes that are especially important in the context of questions about one animal group may not be equally relevant in the context of questions about another animal group. This problem suggests that, instead of attempting to prescribe strict definitions for terms applicable to all animal groups, a more productive alternative is to envisage a continuum. We might adopt an attitude that terms such as ‘social’ are more appropriate for biological attributes closer to one end of the continuum, while at the same time avoiding what Dennett (1996) called ‘definition mongering’. Sometimes, progress in science is facilitated by avoiding misplaced precision. From this perspective, ‘social’ pertains to the behaviour seen when animals interact, ‘sociality’ pertains to the social inclinations of animals and ‘society’ pertains to socially-structured groups. In any particular instance, these terms may or may not assist us in formulating research questions that lead to a better understanding of biological attributes. Precisely what ‘sociality’ and other related terms mean for any species is an empirical question that depends on the outcome of detailed behavioural and ecological research. Another way of saying this is that the appropriate target for precision is in the study of the animal’s biology.

In particular, terminology lifted from research on other animal groups may be inhibiting the asking of basic biological questions about spiders. A number of spider species are acknowledged as being social (i.e., as qualifying for the label ‘social spiders’). At the same time there is now a vast literature about insect sociality. Associated with this literature is a large body of theory that has been guided by background knowledge of the biology of this particularly well-studied animal group. For example, modern theory related to kin selection, inclusive fitness and reproductive division of labour have been shaped to a large extent by extensive background knowledge of the biology of social hymenopterans (ants, bees and

wasps). One approach to research on social spiders has been to adopt the insect-derived definitions and follow through by letting the theory derived from this other animal group shape the questions to be asked about the spiders.

I have chosen a different approach. My starting point is the simple observation that there are some spiders that routinely live and interact together. By using the term 'society' for groups of these spiders, I simply acknowledge that a species appears to be a potentially interesting target for further research concerning the details of what goes on in these groups. Step by step, gaining an understanding of these details will shape evolving research questions and reveal how issues relevant to understanding spiders might converge with issues of importance in the literature on other animal groups.

A fresh perspective on spider sociality might be especially valuable. With this in mind, I investigated species from the family Salticidae. This is the largest spider family, but not a family that has been especially significant in the social-spider literature. Most salticids are hunting spiders (i.e., spiders that do not use prey-capture webs), whereas the social-spider literature has been primarily concerned with web-building spiders. Social web-builders have been likened to sessile, filter-feeding colonies (Uetz et al, 1983). Being active hunters, salticids might more appropriately be likened to wolf packs or lion prides.

The system I chose to study is unconventional in another way as well. The literature on social spiders, and most social animals, has been concerned especially with single-species groups, but many of the social salticids I studied live in mixed-species groups. In a different context, however, mixed-species spider groups have been studied extensively. For example, the spider genera *Argyrodes* (Theridiidae), *Mimetus* (Mimetidae), *Portia* (Salticidae) are well known for species that routinely occupy webs of unrelated species (Jackson 1992). Typically, these occupants of foreign webs have been envisaged as kleptoparasites (Vollrath 1979; Whitehouse 1988; Ramirez and Platnick 1999; Whitehouse and Jackson 1998) or predators (Smith Trail 1981; Jackson and Hallas 1986; Jackson and Pollard 1996), or both (Jackson and

Blest 1982). Kleptoparasitism and predation are examples of exploitation, and it is tempting to envisage exploitation as the antithesis of sociality. This view probably comes largely from the emphasis on ‘cooperation’ in the social-spider literature (Kullman 1972; D’Andrea 1987; Downes 1994). The notion of ‘cooperation’ has an interesting status in the social-spider literature. Although widely used, detail concerning the relevant behaviour and interactions of the spiders, and the consequences of these interactions, are scarce (Jackson 1979; Downes 1995). Here I will adopt a different perspective by acknowledging that, in any particular instance, how single-species interactions compare with mixed-species interactions is an open question. Perhaps ‘cooperation’ and ‘exploitation’ are sometimes overlapping categories.

The mixed-species groups I studied are all from habitats close to the shore of Lake Victoria in Uganda and Kenya, in East Africa. Earlier work has documented the intraspecific communication systems of three of these species (Jackson 1986a, b) and provided preliminary description of colonies from the field (Jackson 1999). However, no previous studies of these species have been concerned specifically with a detailed understanding of sociality. Despite the many obstacles entailed in doing research on African salticids, my objective in this thesis was to extend our understanding of the way sociality has evolved in these unusual animals.

With the African arthropod fauna being only poorly known, systematics has been a particularly significant challenge. In some instances, new species have been described and named in parallel with the research on sociality. Fortunately, in most instances, at least genus names are now available.

Chapter 2 introduces all the salticid species examined in this thesis, describing the general appearance and types of colonies constructed by the social salticids in the field, and the species composition of those colonies. Data from colony surveys conducted in the field are considered in this chapter as a step towards understanding the diverse nature of the colonies and the different species that reside within the nest complexes. The prevalence of mixed-species colonies is highlighted and forms the basis for further investigation in subsequent chapters.

In Chapter 3, I take a more in depth look at the natural history of one particular species, *Portia africana*, an interesting ‘intermediate’ species that appears to have two different social strategies over its lifetime.

In Chapter 4, I examine some of the cues that may influence the joining decisions of *Portia africana* as they participate in cooperative prey capture.

Chapter 5 is a reprint of a taxonomy paper (co-author, Wanda Wesolowska) that names and describes *Myrmarachne melanotarsa*, a social salticid that mimics a social insect, *Crematogaster* (an ant). In Chapter 6, I take a closer look at the natural history of *M. melanotarsa* and provide a basis for the further work in Chapters 7-9. Chapters 7 and 8 deal specifically with the feeding behaviour of *M. melanotarsa*. Chapter 7 deals with prey preferences of this spider species, whereas Chapter 8 examines an unusual behaviour (mouthing of silk) of this species. ‘Collective mimicry’ is investigated in Chapter 9, this being a term I use for groups of this ant-like salticid resembling groups of ants. I examine specifically the potential anti-predator benefit of grouping in this species. Chapter 10 is a study of an unusual foraging strategy of *Menemerus* sp. A, a salticid that steals prey from ants.

Chapter 11 describes the natural history of two salticid-eating reduviid bugs. This chapter is the basis for the following two chapters in which I examine the relationship between the reduviid bugs and the social salticids. Chapter 12 describes the prey preferences of the reduviid bugs, and Chapter 13 compares the ability of the reduviids to prey on solitary and grouped salticids.

Chapter 14 is an experimental study of the joining decisions of the different salticid species I studied and of the cues that the salticids rely on when making their decisions.

In the final chapter, Chapter 15, I return to the question of ‘social’ means in the biology of the East African salticids.

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Chapter 2

Salticid Nest Complexes in East Africa

Abstract

Characteristics of the nest complexes of social salticids are documented from surveys in the field at Mbita Point in Kenya and Entebbe in Uganda. Nine salticid species were particularly often found living in nest complexes, and often more than one of these species were found living together in the same nest complex in a mixed-species group. One species was found living in single-species groups only, while another was found to form female-pair groups only. Associated with the salticid nest complexes, there often were other spider species (especially tetragnathids, hirsutiids and *Portia africana*) and various insects (especially ants and reduviids). Some of the questions raised by the findings from these surveys are investigated in later chapters.

INTRODUCTION

All spiders spin silk, which they use in a variety of ways (Foelix 1996). Webs are perhaps the best-known silk artefact of spiders, and spider webs differ considerably in their details (Shear 1986). Although rarely defined strictly, the term 'web' most often refers to a prey-capture device that is considerably larger than the spider and held in place by silk lines connected to vegetation, rocks, the ground, or other features of the environment (i.e., 'support structures'). Most often, webs are stand-alone silk edifices (i.e., their support structures are not other webs), but there are numerous exceptions, known as 'web complexes' (i.e., when the support structures of webs include other webs, a web complex is formed), and sometimes web complexes can reach enormous size, with as many as 10,000 resident spiders (Jackson, 1979). Whether stand-alone or part of a web complex, the individual web is usually envisaged as a single spider's home, but there are exceptions to this rule as well. For example, adult females often share webs temporarily with newly hatched juveniles (Norgaard 1956; Besseken et al., 1992) or with one or more courting males (Robinson and Robinson 1980), and subadult females often share webs with adult males (Jackson 1986a).

In the literature on web-building spiders, ‘social spider’ is another common term. It is applied to spiders that live in web complexes (Buskirk 1981; Uetz and Cangialosi 1986) and it is also used for when a large number of conspecific individuals routinely share an individual web, colonies of *Stegodyphus mimosarum* from East and South Africa being a dramatic example of this (Seibt and Wickler 1988).

Sometimes individuals belonging to different species may also live together in shared individual webs or in web complexes. Although a subgroup of conspecific individuals within the heterospecific assemblage might be called social, it is not traditional to call the heterospecific assemblage itself a colony of social spiders. For shared individual webs, typically one species is envisaged as having been the builder of the web (the host) and the other resident species are envisaged as kleptoparasites, commensals or predators (Bradoo 1979; Vollrath 1984; Jackson 1986b; Rypstra and Binford 1995; also see Elgar 1989), but attributing the origin of the web to one species is not always straightforward.

For example, *Argyrodes* is a genus of small-bodied theridiid spiders, with some species being well known for sharing webs with much larger host-spider species (Vollrath 1979; Whitehouse 1986; Tso and Severinghaus 2000). Large orb webs of *Nephila* spp. and *Argiope* spp. are especially well known for harbouring *Argyrodes* (Whitehouse 1988; Grostal and Walter 1997). It may be tempting to conclude that *Argyrodes* simply lives on the other spider’s web, overlooking how *Argyrodes* may often be spending much of its time on its own silk (i.e., its ‘support web’ added to the silk of the host spider; Whitehouse 1991). Another example is *Portia*. These web-building salticid spiders (Jackson 1985) routinely build their own web into the webs of other spider species. In the field, it can be exceedingly difficult to discern where *Argyrodes*’s or *Portia*’s web ends and the other spider’s web begins (Jackson and Hallas 1986). These examples show that, contrary to tradition, it is sometimes appropriate to say a web has been built by more than one spider species.

For convenience, we call spiders that do not build webs ‘hunting spiders’, although close scrutiny sometimes makes applying this term awkward. Hunting may suggest a predator that seeks its prey out, but many ‘hunting spiders’ appear to wait for their prey to pass by and then make a sudden ambushing attack (Morse 2000; Li et al. 2003). Web-building spiders may sometimes capture prey outside their webs (Jackson 1986b; Li et al. 1999). Many hunting spiders build silk nests (typically tightly woven tubular structures, not much larger than the resident spider) that they use as shelters, not as prey-capture devices, although closer scrutiny sometimes reveals nests playing a role during predatory sequences (Jackson and Macnab 1989; Jackson 1990). Besides secluding themselves inside nests when quiescent, hunting spiders may also use their nests as sites for moulting, mating and oviposition.

What applies to the webs of web-building spiders may also apply to the nests of hunting spiders: nests are usually envisaged as stand-alone structures occupied by solitary individuals, but sometimes hunting spiders join nests to other nests, making nest complexes. My particular interest has been the nest complexes of jumping spiders (Salticidae).

Vision is poorly developed in most spiders but salticids have unique complex eyes and exceptional eyesight, with the spatial acuity of salticid eyes approaching that of primates (Land 1969; Forster 1982; Blest et al 1990). Although most salticid species appear to be hunting spiders, with stand-alone nests being typical, there have been reports of at least rudimentary sociality in salticids.

In Venezuela, Crane (1949) found 14 individuals of the salticid species, *Semorina megachelyne* (adult males, adult females and juveniles of various sizes), living in a single “large silk shelter”, as well as individuals of the salticid, *Corythalia xanithopa*, living in clusters of 3-10 individuals. There have also been scattered reports of salticids in temperate regions forming over-wintering aggregations, typically with the salticids in touching, but individually occupied, nests under loose bark of trees, beneath stones on the ground and on doorjambs (Kaston 1948; Jennings 1972). These aggregations contain as many as 50 individuals, and there may be several

salticid species, and even spiders from other families, in a single aggregation. Some temperate salticids may form similar aggregations in the summer (Kajak and Luczak 1961; Luczak 1971). However, few details concerning any of these salticid aggregations have been available.

Especially large nest complexes have been described from the shore of Lake Victoria at a site near Kisumu in western Kenya. These complexes, occupied by three unidentified species of *Menemerus* and two unidentified species of *Pseudicius* (Jackson 1986a, b), consist of individually discernible nests, which are bridged by interstitial silk and woven together into a continuous silk mat on trunks, branches and leaves of trees, on buildings, and on boulders. Sometimes hundreds of individual salticids occupy single nest complexes, although 40-50 is more common. Nest complexes occupied by these same species, as well as some other salticid species, have been found at another two locations on the shore of Lake Victoria (Jackson 1999), Mbita Point in Kenya and Entebbe in Uganda. Although these social salticids appear to be part of an especially complex system (Jackson 1999), there have been no detailed studies on their biology.

As a first step, I use field data here to characterize nest complexes. Rather than systematic sampling and detailed statistical analyses, the goal here is something more elementary: an objective demonstration of the kinds of nest complexes that occur in nature. This includes providing details about the size and composition of salticid populations within complexes, identifying the different types of complexes, and documenting the microhabitat associations of the different kinds of salticid nest complexes. These are baseline data from which more specific research objectives are developed for investigation in later chapters.

MATERIALS AND METHODS

Data on salticid complexes came from two sites, each site extending for about 200 m inland from the shore of Lake Victoria. Elevation at each site was about 1100 m and latitude was between 1°N and 1°S.

Entebbe

This site was in the Entebbe Botanic Gardens, at the northern end of Lake Victoria in Uganda (0°04'N, 32°29'E, altitude: 1182 m). With a mean annual rainfall of approximately 1500 mm (Rome Pearce and Smith 1998), the habitat here was closed-canopy rainforest alternating with more widely spaced trees (open canopy) in maintained gardens filled with a great variety of native and introduced tree species.

Mbita Point

This site was the grounds of the Thomas Odhiambo Campus (TOC) of the International Centre for Insect Physiology and Ecology (ICIPE): Mbita Point, Kenya (0°25'S, 34°12'E, Altitude: 1148 m), situated about midway along the east shore of Lake Victoria. Mean annual rainfall recorded at the nearest station (Kisumu) is 1141mm (Rome Pearce and Smith 1998). The habitat is widely spaced trees (open canopy) in maintained gardens. Dominant trees include frangipani, mango, fig and citrus.

Sampling

Sampling was carried out opportunistically, the procedure being simply to record data on complexes when they were found. A 'colony' was defined as the residents of a single nest complex and six microhabitats for colony location were recognised. Records of colonies in three of these microhabitats were especially common: tree trunks, the surfaces of leaves, and the walls of buildings (Fig 2.1). Records from another three microhabitats were not so common: deserted wasp nests, leaves suspended within the webs of *Cyrtophora* sp. (Araneidae) (dome-like webs especially common in the vegetation of citrus trees) (Scharff and Coddington 1997), and leaves suspended in the webs of *Nephilengys* sp. (Tetragnathidae) (orb webs close to trunks of large

trees) Japyassu & Viera, 2002). Both *Cyrtophora* and *Nephilengys* build large, detritus-cluttered webs.

When colonies were found, the silk of the nest complex was teased apart with forceps ('dissection') and data on the occupants recorded. Nest complexes that could not easily be collected in their entirety were dissected *in situ* after placing a sheet of cardboard directly below the nest complex (any salticids that decamped from the nest complex landed on the cardboard, where they could be easily seen and collected). Sometimes colonies found on leaves were collected in their entirety (intact on the leaves), placed in plastic vials or plastic bags and then taken to the laboratory where the leaves were placed in a large plastic tray before dissection.

At Mbita Point, a total of 408 nest complexes were surveyed. These included 136 nest complexes on tree trunks and limbs ('bark colonies'), 114 nest complexes on leaves ('leaf colonies'), 89 nest complexes on the outside walls of buildings ('wall colonies'), 21 nest complexes in old wasp nests ('wasp-nest colonies'), 34 nest complexes on leaves in *Nephilengys* webs ('*Nephilengys* colonies') and 14 nest complexes on leaves in *Cyrtophora* webs ('*Cyrtophora* colonies'). Surveys included an additional 472 solitary nests (252 on walls, 106 on tree trunks, and 114 on leaves), where these nests contained salticid species that were usually found in nest complexes.

In Entebbe, a total of 217 nest complexes were surveyed. These included 175 nest complexes on leaves and 42 nest complexes on walls. An additional 79 single-species nest complexes were also surveyed and an additional 177 solitary nests containing salticid species usually found in nest complexes were also surveyed (all found on leaves).

RESULTS

Nine species were prevalent in the sampled complexes: two species of *Myrmarachne* (*Myrmarachne melanotarsa* and an unidentified species called, for convenience, '*Myrmarachne black*'), two unidentified species of *Pseudicius* (hereafter called sp. A. and sp. B), and three

unidentified species of *Menemerus* (hereafter called sp. A, sp. B, and sp. C), a species resembling *Hasarius* (hereafter called ‘the Nun’) (Uganda only), and *Parajotus cinereus* (Uganda only). The ‘Nuns’ and *P. cinereus* were typically found in single-species complexes (42 for Nuns and 37 for *Parajotus*) or in complexes that were almost single-species. However, most of the salticids were found in multi-species nest complexes, with the occupants being highly variable assortments of species.

Bark colonies (Fig 2.1.a) were found especially in fig trees (*Ficus* sp.). Areas of tree trunks broken or scarred by limb removal were especially common nest-complex sites. Wall colonies (Fig 2.1.b) were common despite the efforts of cleaning staff to remove them. Leaf colonies (Fig 2.1.c) were especially common on frangipani (*Plumeria* sp.), mango (*Mangifera* sp.), fig (*Ficus* sp.), and citrus trees. The leaf colonies were found on the surfaces of green leaves and also within the enclosed spaces made by curled-up dry leaves. The dry leaves were often anchored to the tree by silk.

The size of the colonies varied greatly, with some apparent trends across microhabitat being evident (Table 2.1). Colonies of 4-10 individuals were especially common in all microhabitats, but colonies of 25 or more were found primarily on walls and tree trunks, and in wasp nests (Fig 2.1.d).

At Mbita Point, the largest colonies (>50 individuals per nest complex) were found in empty wasp nests. There were also some especially large colonies (>35 individuals per nest complex) on tree trunks and walls. Colonies on leaves tended to be small (typically about 4 or 5 individuals per complex). Compared to Mbita Point, Entebbe wall and leaf colonies, tended to be larger (13.2 S.D.±9.5 individuals per colony in wall habitats and 8.5 S.D.±6.3 in leaf habitats).

More than one species living together in colonies was typical (Fig 2.2), two or three species being the norm, but colonies in almost all the habitats sometimes had four or more resident species. Except for *P. cinereus* and ‘Nun’ salticids, single-species colonies were the exception.

Nest complexes and web complexes

Orb webs of *Tetragnatha* sp., *Nephila* sp. and *Nephilengys* sp. (Tetragnathidae) and dome webs of *Cyrtophora* sp. (Araneidae) were especially common at Mbita Point, with the 3-D webs of *Argyrodes* p. enmeshed, and difficult to discern, within the webs of these larger spiders. The webs of all of these species tended to run together, forming large interspecific web complexes on the vegetation, on tree trunks, and on neglected walls of houses and other buildings. Web complexes on tree trunks were especially often concentrated within hollows created by branches that had been removed. Salticid nest complexes, in turn, often merged with the silk of the web complexes. Salticid nest complexes associated with webs were found especially often in the silk surrounding old egg sacs of the web spiders, silken retreats (i.e., the nests built by the web-builders), or in masses of disused frame threads and silk from barrier webs (Fig 2.3). Many nest complexes were fastened to web silk alone.

Bark Colonies

Many bark colonies were small, but some very large colonies (not surveyed) were also found, occupied by hundreds of individuals. The colonies surveyed at Mbita Point were dominated by *M. melanotarsa*, with notable numbers of *Pseudicius* sp. A, *Pseudicius* sp. B, and *Menemerus* sp. A.

M. melanotarsa was found almost exclusively in bark colonies, with wasp nests being the primary exception. Whenever *M. melanotarsa* was found in a bark colony, numerous ants (*Crematogaster* sp.) were also present. *M. melanotarsa* resembles *Crematogaster* sp. in size and general body form. Often colonies occupied by *M. melanotarsa* were close to the locations where *crematogaster* ants were also abundant and active.

Bark colonies were especially often built around old eggsacs of *Hersilia caudate*, a bark-dwelling spider (Hersiliidae) that ambushes prey and builds silken eggsacs on tree trunks (Filmer 1991, Metwally et al 2001). Small salticid bark colonies appeared to have been constructed in many cases within the existing silk of either abandoned or still occupied eggsacs of these hersiliids (Fig 2.4).

Large and small colonies appeared to have similar species living in them. Larger colonies simply had larger numbers of individuals of all types, but larger colonies also tended to have more extraneous residents that were not salticids including, especially, an unidentified gnaphosid spider species. *Portia africana*, a salticid that does not build nests, was found primarily in larger colonies. *Crematogaster* sp. and other ants were often seen walking on the silk of the nest complexes (Fig 2.5).

Wall Colonies

The wall colonies in Mbita Point and in Entebbe were dominated by *Menemerus* sp. A, although notable numbers of *Menemerus* sp. B, *Menemerus* sp. C and *Pseudicius* sp. A were also present. The nest complexes were often found in the narrow channels between the brickwork on the outside of buildings (Fig 2.1.b.), often near trails of *Crematogaster* sp. Often the colonies on walls were built around the silk from disused and in-use nests and webs of non-salticid spiders, including oecobiids, clubionids and various other unidentified families.

Leaf Colonies

Colonies were often on the leaves of the various trees in Mbita Point and Entebbe. With space being limited on the leaf surface, these colonies were generally the smallest of those found in the three habitats. In Mbita Point and in Entebbe, leaf colonies were dominated by *Pseudicius* sp. A, with notable numbers of *Pseudicius* sp. B, *Menemerus* sp. A, and the black *Myrmarachne* sp. also being present. Often there were ants on the surfaces of leaves. Reduviids (*Nagusta* sp. and *Scipinnia repax*) were also common in these complexes. Nest complexes were often located

near eggsacs and web silk of *Tetragnatha* sp. that had accumulated on leaf surfaces (Fig 2.6). Old lepidopteran pupa cases were often found in close proximity to the salticid nest complexes, sometime with salticids having their nests inside.

Wasp-Nest Colonies

The wasp-nest colonies at Mbita Point were dominated by *Pseudicius* sp. A. These colonies were in old wasp nests hanging from house awnings. The salticids had their nests embedded in the cells of the wasp nest.

Salticids in Solo Nests

No individuals of *Myrmarachne melanotarsa* were found in solo nests, but all other species were sometimes found in solo nests. On walls and on tree trunks, males appeared to account for an especially large proportion of the occupants of solo nests for all species. Adults of both sexes of *Menemerus* sp. C were especially often found in solitary nests on walls. For the Nuns and *P. cinereus*, it was the males and juveniles that tended to be found in solo nests, whereas adult females tended to be more strictly occupants of nest complexes. Nest complexes of the Nuns were typically occupied by only two females.

DISCUSSION

There is a strong tradition in the literature on social spiders (Kullman 1968; Downes 1994), and on animal sociality in general, of orienting definitions and theory towards issues related to single-species groups. Yet there have also been reports of spiders living in mixed-species groups (Krafft 1970; Hodge and Uetz 1992,1996), and the prevalence of multi-species salticid colonies in the two East African study sites suggests that a break with the spider literature's single-species tradition might be instructive. This thesis is an initial step toward exploring where the break with tradition might lead when considering salticid sociality.

However, with so many different species being found in the nest complexes, along with various non-salticid spiders and various insects, it was necessary to choose for further study some particular potential relationships between species suggested by the field surveys.

Portia africana is of particular interest, as this species is known to prey especially on other spiders (Li et al. 1997). The relationship between this araneophagic salticid and the other social salticids is considered in Chapter 3 and how individuals of *P. africana* hunt together is considered in Chapter 4.

Myrmarachne melanotarsa is another salticid that stands out. How this social ant-like salticid interacts with its social model, *Crematogaster*, and with the other salticids is considered in Chapters 6-9. *Menemerus* sp. A. also appears to have an unusual relationship with ants (it steals prey from ants). This is the subject of Chapter 10.

Assassin bugs (Reduviidae) appear to be unwelcome guests in the salticid nest complexes. They prey on the salticids. Unusual specialization by these predatory bugs on salticids, and on each other, is investigated in Chapters 11-13.

These chapters on special topics are followed, in Chapter 14, by an experimental study designed to ascertain whether the nest-complex salticids make active decisions to join other conspecific and non-conspecific salticids.

Fig 2.1 Examples of salticid nest complexes in four different habitats.



2.1.a. Bark colony



2.1.b. Wall colony



2.1.c. Leaf colony



2.1.d. Wasp nest colony

Table 2.1. Colony Size (number of occupants per salticid nest complex)

Study Site	Habitat	N	Mean	Standard Deviation (±)	Maximum	Minimum
Mbita Point	Tree Trunk (Bark)	136	8.8	7.67	41	2
	Wall	89	7.5	6.3	38	2
	Leaf	114	4.6	3.0	31	2
	Wasp nest	21	28.4	22.7	77	4
	Leaf in <i>Cyrtophora</i> sp. Web	14	4.1	2.2	9	2
	Leaf in <i>Nephilengys</i> sp. Web	34	4.1	2.7	16	2
Entebbe	Wall	42	13.2	9.5	39	2
	Leaf	175	8.5	6.3	41	2
	<i>Parajotus</i> <i>cinereus</i> colonies	38	6.0	3.1	15	2
	Nun salticid colonies	43	2.9	1.1	6	2

Fig 2.2. Number of species per colony in ten different habitats

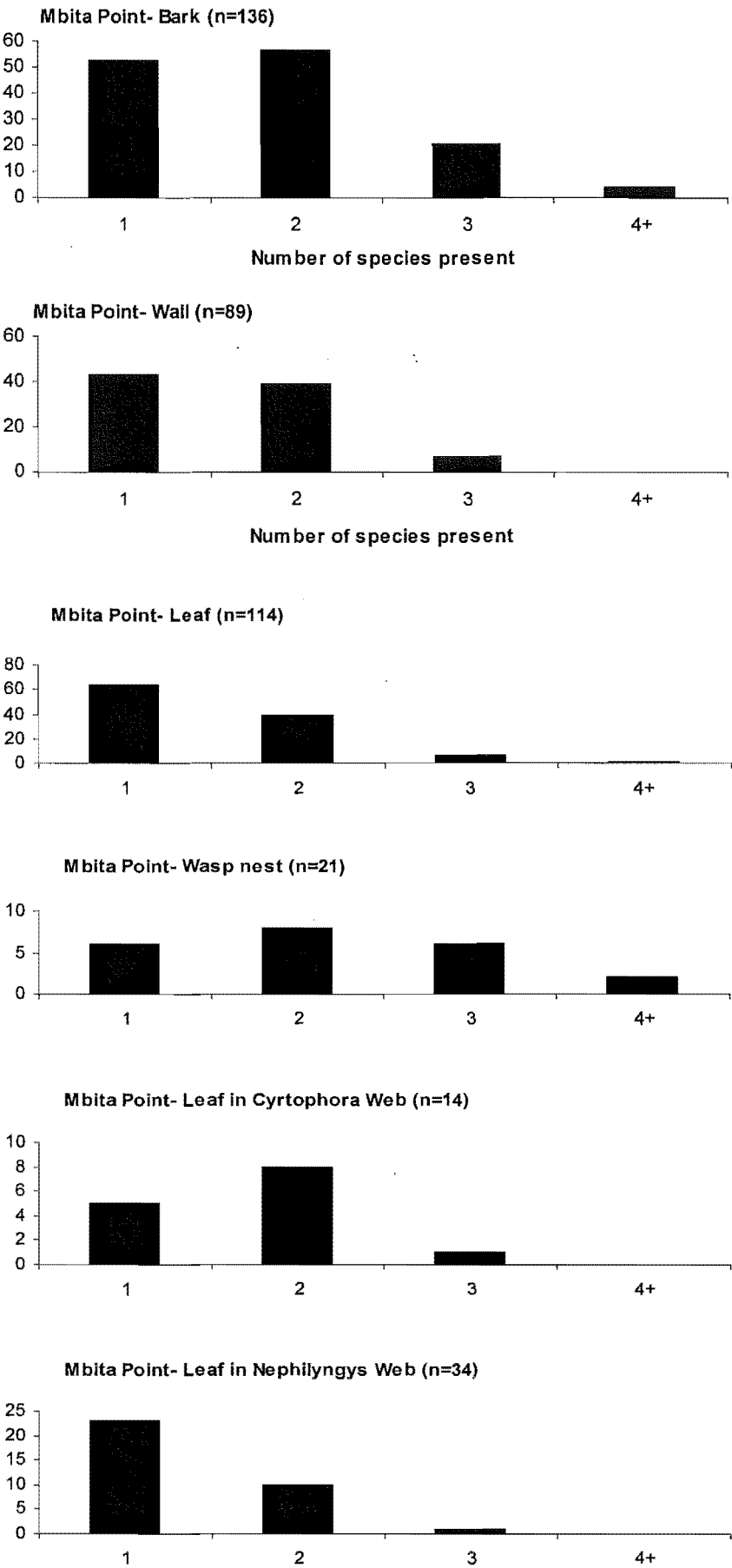


Fig 2.2. cont...

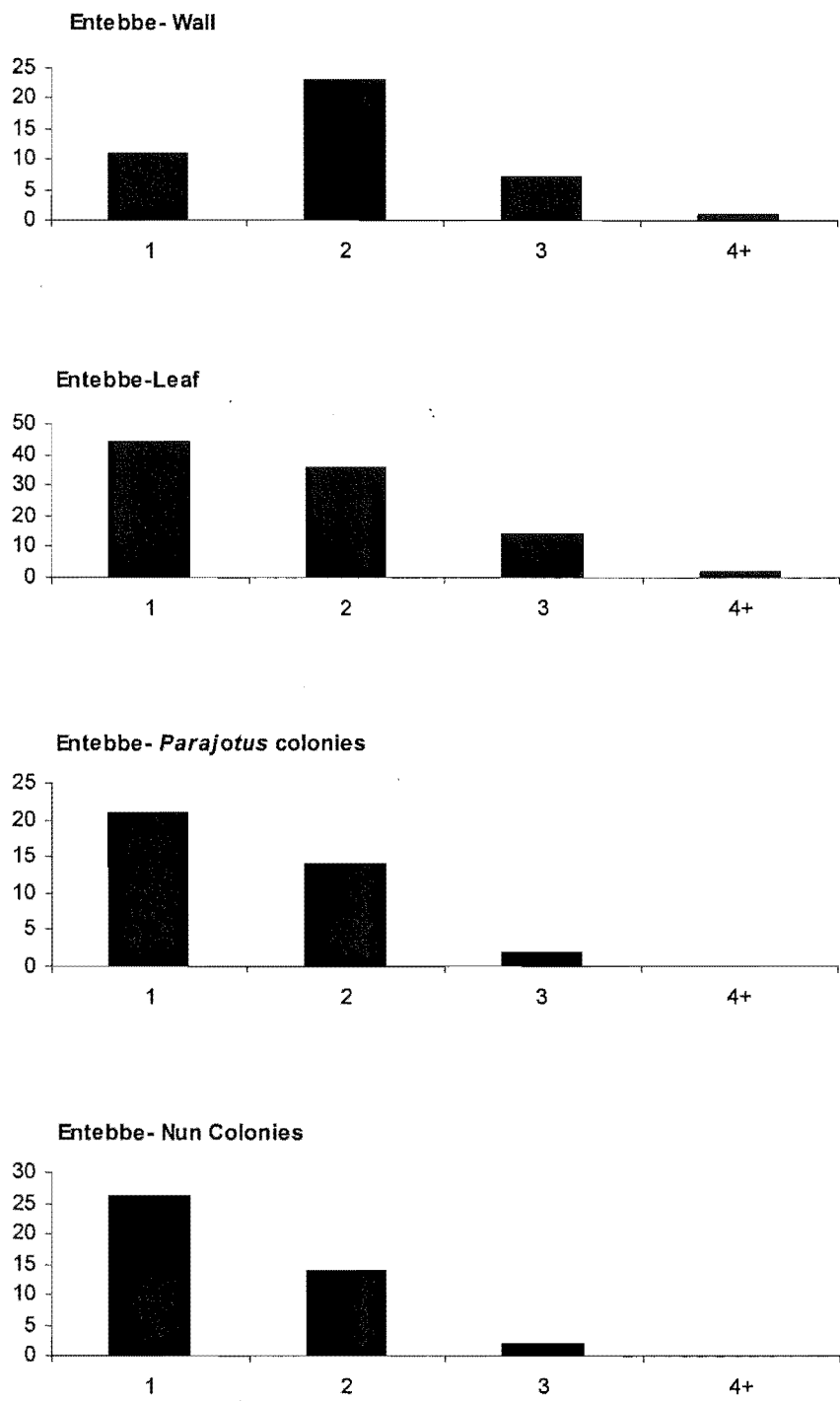




Fig 2.3. Salticid nest complex, in bark habitat, embedded in web silk of web-building spiders



Fig 2.4. Nest complex built in bark habitat on hersiliid silk (with hersiliid present)



Fig 2.5. *Crematogaster* ants on the surface of a salticid nest complex (bark habitat).



Fig 2.6. Nest complex within *Tetragnatha* sp. webbing (leaf habitat)

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Chapter 3

Observations in the field of social groups of *Portia africana*, an araneophagic jumping spider

Abstract

Instances are documented of finding individuals of *Portia africana*, an araneophagic jumping spider, living clustered together in the field in webs, in nest complexes of other salticids, around solitary nests of other salticids, and around the nests of oecobiid spiders. Adult males and females, as well as juveniles of all stages, were sometimes aggregated. Sometimes they also fed together on the same prey, but it was the early-instar individuals that especially often aggregated and especially often practised joint feeding. Small *Portia* juveniles surrounded the nests of other salticids and of oecobiid spiders. When the resident oecobiid or salticid attempted to leave or enter the nest, one of the *Portia* juveniles sometimes lunged and captured it. Subsequently, other *Portia* individuals from around the nest occasionally joined to feed.

INTRODUCTION

Jumping spiders (Salticids) have unique, complex eyes and acute eyesight (Land 1969, 1974, Jackson and Blest 1982, Blest 1985). Most salticid species are hunting spiders (i.e. they do not live in webs) and feed primarily on insects (Richman and Jackson 1992). However, there has been considerable interest in the salticid genus *Portia*, because this is a genus in which remarkable behavioural complexity and predatory versatility have evolved (Jackson and Pollard 1996). Besides hunting cursorially, the species from this genus build prey-capture webs, invade the webs of other spiders, practice aggressive mimicry and prey on other spiders (Jackson and Wilcox 1998). Here I consider something new for *Portia*, sociality.

In East Africa, juveniles of *Portia africana* often live inside nest complexes built by other salticids (Chapter 2). Here I present opportunistic natural-history observations from the field, as well as more structured observations from the laboratory. The baseline information from this chapter generates hypotheses that are considered in later chapters.

MATERIALS AND METHODS

Field Observations

The field site was Mbita Point (Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology) in Kenya and the Entebbe Botanical Gardens in Uganda. Opportunistic observations were made at different times during the day whenever *Portia* was found, with each observation period lasting 20-120 min. However, *P. africana* was present in four especially large complexes at Mbita Point (referred to as the 'primary complexes'), and these were observed repeatedly (almost daily) over a period of three months. Each was a combination, a large web complex and several nest complexes running into the silk of the large web complex, with other smaller, and disconnected, web and nest complexes nearby ('satellite complexes'). The webs were built by *P. africana* and by a number of other spider species, but especially *Nephilengys* sp., *Cyrtophora* sp., and *Tetragnatha* sp.

Laboratory Observations

Laboratory cultures were established from individuals of *P. africana* collected in the field at Mbita Point (Kenya) and Entebbe (Uganda), with standard spider-laboratory rearing and maintenance procedures (Jackson and Hallas 1986) being adopted. *P. africana* juveniles from these cultures were maintained in groups ('colonies') of 5-20 in large cages (about 1 x 1 x 1.5 m, made from wood and glass), each colony being maintained for approximately two months. Four types of groups were established: sibling spiderlings from the same eggsac (i.e., no adults present), unrelated spiderlings (i.e. spiderlings that had different parents; no adults present), groups of unrelated adults (no spiderlings present), and adult females accompanied by their own progeny.

Web-building spiders were introduced to the cages and allowed up to three days to establish some webbing within the cage environment before introducing *P. africana*. For web-building spiders, *Nephilengys* sp. from *P. africana*'s habitat in East Africa was used, along with various other species collected locally. Pieces of wood (arranged horizontally and diagonally in

the cages) served as web-connection points and multi-level platforms on which salticids could sit. For prey, vinegar flies (*Drosophila melanogaster*), houseflies (*Musca domestica*), mosquitoes (*Anopheles gambiae*) and lake flies (Chaoboridae and Chironomidae) were added *ad libitum*. Various web-building spiders found locally were also added as prey.

Definitions

‘Spider A’ was the first spider to capture and begin feeding on a prey item. Whenever comments were made about Spider A, this spider was actually feeding on a prey item at the time, unless specifically stated otherwise. Spiders B, C, D, and so on were individuals that subsequently joined Spider A at the prey, with successive letters indicating the sequence in which they joined.

An ‘observer’ was a spider that oriented, and remained oriented, towards Spider A, but did not move towards Spider A. An ‘approacher’ was a spider that was oriented to, and moved directly towards, Spider A. An approacher either ‘failed’ (i.e., it was unsuccessful in joining with Spider A in feeding) or ‘succeeded’ (i.e., it managed to feed with Spider A). A successful approacher, once it began feeding, then became Spider B, C, D and so on. The laboratory was maintained under a controlled photo-period (12L: 12D), temperature (c 25°C) and relative humidity (80%).

‘Usually’, ‘sometimes’ and ‘occasionally’ are used to indicate frequencies of occurrence of >80%, 20-80%, and <20%, respectively. Spiders were classed into three size groups. ‘Small juveniles’ were from the first two instars out of the eggsac (body length 1-2 mm), ‘large juveniles’ were larger than small juveniles but not yet adults (body length >2 mm), and adults were >10 mm in body length.

RESULTS

Field observations of P. africana in salticid nest complexes

Each time they were observed, all three of the primary nest complexes had at least one adult female of *P. africana* present, usually within a combination of its own web and a web built by one or more of the other web-building species present in the web complex. The webs in turn surrounded salticid nest complexes. Sometimes *P. africana* adults were seen actually on the salticid nest complex silk. There was one complex at which at least three adult females of *P. africana* were usually present, with these being either all in the main complex or else with one or two in satellite complexes.

In each of the primary complexes, small juveniles (1st to 3rd instar) of *Portia* were always present either on web silk or on the surface of nest complex. *P. africana* juveniles were also commonly seen clustered in other nest and web complexes in the field.

Ambushing of prey and feeding together

In the laboratory, there were two instances of seeing adult females of *P. africana* feeding together: (1) feeding together on an *Eriophora pustulosa* female (an orb web spider: Araneidae); (2) feeding together on another adult *P. africana* female. How the cannibalised conspecific died is not known. It was considerably more common to observe juveniles feeding together, and the majority of observations of feeding together were of small juveniles of *P. africana* feeding together on *Oecobius amboseli*, a spider species found on tree-trunks, stones and the walls of buildings at Mbita Point. Like other oecobiids (Shear and Benoit, 1974), *O. amboseli* builds a silk sheet ('nest') (diameter, about 30 mm) and uses the nest both as a shelter and as a device for detecting prey. When disturbed, *O. amboseli* evacuates the shelter and dashes away.

In the field, *P. africana* juveniles were seen in small groups clustered around the nests of *O. amboseli*. In the laboratory, small *P. africana* spiderlings readily clustered round oecobiid nests and then remained quiescent. Occasionally, one of the *P. africana* spiderlings used its legs

or palps to probe the silk of the oecobiid's nest. Eventually, when the resident *O. amboseli* came out of the nest, the nearest *P. africana* lunged and often captured it. If this attempt failed, the *P. africana* spiderlings tended to remain at the nest. When *O. amboseli* returned later, it often got caught by one of the waiting *P. africana*. *P. africana* juveniles were also seen in the field waiting in small groups around solitary salticid nests. In the laboratory, they captured salticids in sequences similar to those seen in tests with oecobiids. Once an oecobiid or salticid was captured, other *P. africana* spiderlings in the group often moved in and attempted to feed on the *O. amboseli*, alongside the successful *P. africana* spiderling. Although two was the most common number of *P. africana* individuals to share a prey item, occasionally three (Fig 3.1) or even four individuals shared.

Often a *P. africana* juvenile repeatedly approached Spider A, but Spider A kept moving away, taking the prey with it, and the other *P. africana* juvenile eventually gave up. When prey sharing did occur, the prey was in body length usually about equal to and as much as 20% larger than the *P. africana* juveniles. This typically came about by one or more other individuals orienting towards Spider A moving slowly towards Spider A. Spider B usually moved around so as to approach the captured prey from the side opposite to the side from which Spider A was feeding. Spider B then moved in close and grabbed hold of the prey. Spider A sometimes stepped away one or more times before Spider B could reach it, but eventually Spider B approached from the opposite side and began to feed. Sometimes Spider A dropped the prey item and ran towards Spider B, with Spider B's response being to flee, only to return later. After Spider B began feeding, there were often repeated episodes of Spider A placing its legs on and pushing Spider B, all the while holding on to the prey.

DISCUSSION

Finding *P. africana* in groups within web complexes and nest complexes of other species raises questions about the specific advantages *P. africana* might gain by being within web and nest complexes of other species and about the specific advantages of clustering with

conspecifics. For all the various species that live in web and nest complexes, including *P. africana*, the mass of jointly-made silk may be a significant barrier against the attacks of various predators. However, for *P. africana* living in this spider-built environment there may also be feeding advantages. Many of the inhabitants of web and nest complexes appear to be *P. africana*'s prey, and joining other individuals of *P. africana* may often enhance the joiner's access to prey.

For *P. africana* juveniles, clustering with other *P. africana* juveniles may also be advantageous for predation on spiders not in complexes, particularly *O. amboseli*. *P. africana* juveniles clustered around the nests of *O. amboseli* and fed on the resident oecobiid, suggesting that clustering functions as a social predatory tactic. By surrounding the nests of *O. amboseli*, *P. africana* ambushed these spiders as they attempted to go in or out of the nest. The laboratory observations suggest that, even when another *P. africana* juvenile actually captures the oecobiid, sharing is a possible reward for the *P. africana* individuals that joined. In Chapter 4, this potential predatory tactic of *P. africana* is examined experimentally.

That *P. africana*'s inclination to feed together diminishes as juveniles get older and larger is suggested by the field data (i.e., sharing of prey was seen more often among early-instar juveniles). Field and laboratory observations also suggested that prey sharing was not always a peaceful concordance, as it was often preceded by attempts by the individual with the prey to move away and, after sharing began accompanied by individuals pushing at one another. When sharing did occur, it appeared that the size of the prey item usually prevented Spider A from moving away quickly enough. Something similar has been described for prey sharing by *Argyrodes flavipes*, a web-building social theridiid spider (Whitehouse and Jackson 1998). As for *A. flavipes*, prey sharing by *P. africana* juveniles suggests a sociality-kleptoparasitism continuum, with prey sharing being more like a consequence of two spiders reluctantly reaching a truce rather than two spiders working together toward a mutually agreed upon goal.

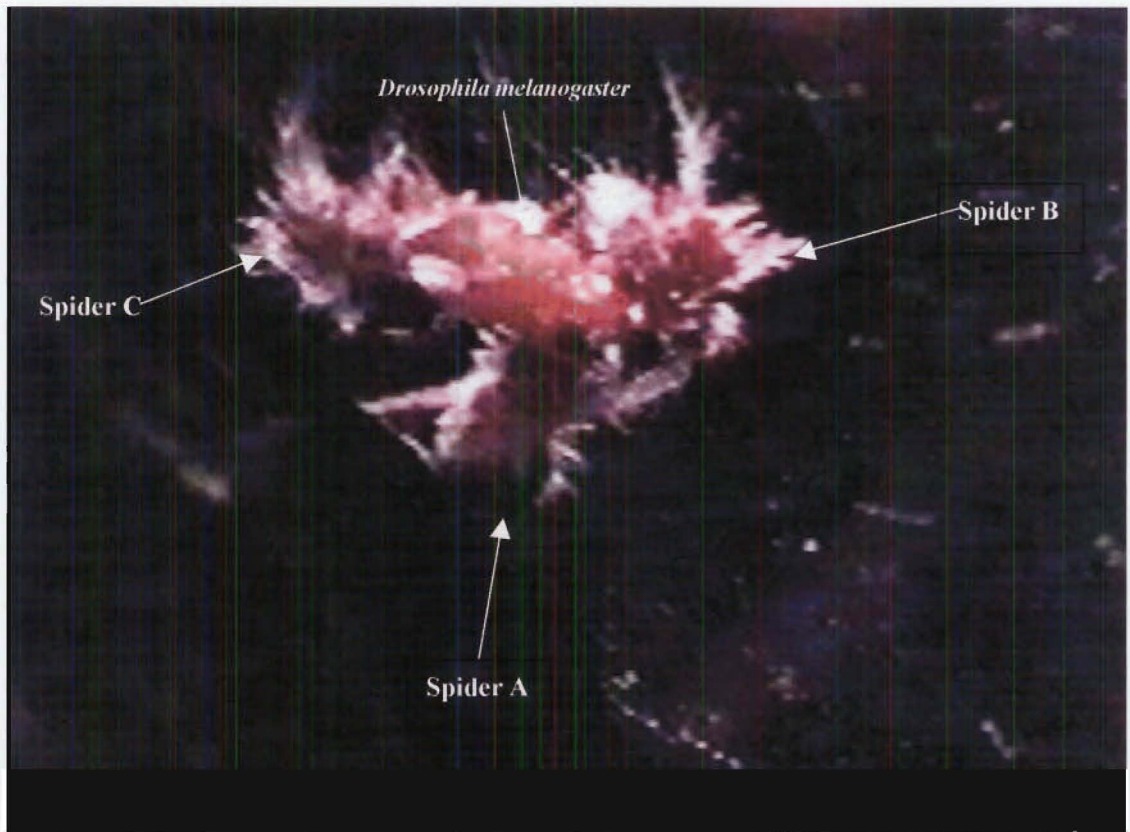


Fig 3.1. Three 2nd instar juveniles of *Portia africana* feeding together on *Drosophila melanogaster* (frame from video recording)

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Chapter 4

Spiders that count: Cues influencing joining decisions during cooperative prey capture by *Portia africana*, an araneophagic jumping spider

Abstract

Portia africana juveniles prey on *Oecobius amboseli* by settling around nests and ambushing the oecobiid as it leaves or returns to the nest. More than one *Portia* juvenile may join at nests. Experiments carried out using lures made from dead spiders mounted in lifelike postures on corks were used to investigate the cues that influence *Portia*'s decisions during encounters with oecobiids and other *Portia*.

INTRODUCTION

Optimal foraging theory (MacArthur and Pianka 1966, Pyke *et al.* 1977, Stephens and Krebs 1986) suggests that animals are adapted to maximize their net energy intake, and often there is an implication that animals are making decisions based on information about one amount being larger than another. Ordinality and numerosity are more specific abilities (Shettleworth 1998). Experimental studies of primates (Hauser *et al.* 1996, Uller *et al.* 2001, Sulkowski and Hauser 2001, Santos *et al.* 2002) and parrots (Pepperberg and Shive 2001, Pepperberg and Wilcox 2002) have demonstrated at least limited ability to add and subtract small numbers, as well as ability to discern, within an array of different objects, the number of objects with specific characteristics. However, what optimal foraging theory especially seems to suggest is that the capacity for ordinality would often benefit animals in nature. Ordinality can be envisaged as an animal recognizing that one number is greater than another ($2 > 1$, $3 > 2$, $4 > 3$, and so on) (Shettleworth 1998), while acknowledging that animals do not conceptualize numbers using words the way we do (Pepperberg 1988, Trick and Pylyshyn 1994). However, ordinality implies at least a rudimentary ability to use information about numbers (Hauser and Carey 1999).

Although experimental studies of the ordinality abilities of a wider range of animals would be useful, the primary non-mammal and non-bird example has been a study of another

vertebrate, a salamander (Uller *et al.* 2003). Experimental studies of arthropod ordinality would be particularly interesting.

In animal studies, including the salamander study (Uller *et al.* 2003), there has been a tendency to consider primarily situations in which the animal ‘goes for more’ (i.e., when given a choice between smaller or larger numbers of items that are attractive to the test subject, the larger amount or number is chosen). The salamander, for example, was accurate in choosing two instead of one or three instead of two, but it appeared to have considerable difficulty with numbers beyond three. African grey parrots have difficulty with numbers above six or seven (Pepperberg 1994, 1999), and six or seven may tend to be the limit for non-human primates, human infants and for human subjects discerning numbers in situations where they can not rely on verbal language for counting (Whalen *et al.* 1999, Feigenson *et al.* 2002, Hauser *et al.* 2000).

Although largely neglected in experimental studies, there are situations in which predators may ‘go for less’. For example, a predator foraging in a group may run the risk of losing a share of the prey it captures when the group size is larger (Clark and Mangel 1986). Many predators are also scavengers (Kruuk 1972, Packer 1986), and scavenging amounts to stealing when the scavenging individual takes all or part of a meal away from the individual that made the kill. When deciding whether to join a group, ‘going for less’ (i.e., going for fewer rivals) may often be advantageous.

Recent studies of encounters between *Portia africana* (Chapter 3), an araneophagic salticid spider from East Africa, and *Oecobius amboseli* (Oecobiidae), a common spider in the same habitat as *P. africana*, suggest that rudimentary numerosity might apply to arthropods as well as to vertebrates and that *P. africana* operates with rules that are more specific than ‘go for more’ or ‘go for less’.

Oecobius amboseli builds small (diameter 2-3X body length of occupant), sparsely-woven tent-like nests on boulders, tree trunks and the walls of buildings. When prey contacts the nest, *O. amboseli* dashes out, runs circles around the prey and wraps it up. When disturbed by a

potential predator, the oecobiid runs in a straight line away from the nest, freezes, and later walks back and enters the nest. *O. amboseli*, like most spiders (Land and Nilsson 2002), has simple eyes and poor eyesight, but salticids have complex eyes and high-acuity vision (Land 1974, Williams and McIntyre 1980) with which they can identify prey from a distance (Harland and Jackson 2001, 2004). The exceptional eyesight of salticids is critical for the experimental design adopted here for investigating the cues that influence *P. africana*'s decisions during encounters with *O. amboseli*.

Small juveniles (first and second instar) of *P. africana* routinely settle close to the nests of *O. amboseli*, often joining with one or more other *Portia* juveniles (Chapter 3). After one of the *P. africana* juveniles captures an oecobiid that is attempting to leave or return to its nest, the other juveniles may be successful at feeding alongside the individual that made the capture. The oecobiids and the *P. africana* juveniles are similar in size, and it would appear difficult for more than two feeding *P. africana* juveniles to fit around a single captured oecobiid. It is rare to see more than two *P. africana* juveniles feeding together and groups of more than two juveniles waiting at an oecobiid's nest are rare.

Here I present the findings from an experimental investigation of the details that influence the decisions made by *P. africana* juveniles during encounters with *O. amboseli*. The details considered are the numbers, identities, locations, combinations and orientations of the spiders encountered.

MATERIALS AND METHODS

Spiders for this study originated from the Mbita Point (Thomas Odhiambo Campus of the International Center for Insect Physiology and Ecology) in western Kenya, situated on the shore of Lake Victoria. Test spiders were juveniles (body length, 2 mm) of *P. africana* taken from

laboratory cultures. As in numerous earlier studies, (e.g., Jackson and Hallas, 1986), standard maintenance procedures, cage design, basic testing methods and terminology were adopted.

During experiments, instead of test spiders being presented with living prey and living conspecific individuals, they were presented with dead spiders mounted in lifelike postures on corks (diameter at narrow end, 25 mm). The mounts were made from adult females of *O. amboseli* (body length, 2 mm) and juveniles of *P. africana* (body length, 2 mm). *O. amboseli* was collected from the field as needed, and *P. africana* juveniles used for mounts came from the laboratory cultures. There were 13 arrangements of mounts made from dead spiders. Each different arrangement was called a 'scene' (100 replicates for each) (Table 4.1), and each scene was defined by the number, type and configuration of mounted spiders present on the cork, as well as by whether one of the spiders was covered by silk. The silk used was always taken from oecobiid nests and it was placed over a spider to simulate an oecobiid nest. The simulated nest was 4 mm in diameter and only clean silk was used (i.e., the silk was taken from oecobiids that had been kept in the laboratory for 7 days without prey prior to silk collection).

Standard methods for making mounts were adopted, as described elsewhere (e.g., Li and Jackson 1996). The same individual test spider, dead spider on a mount, or simulated nest was never used in more than one test. Data from some sets were pooled when not significantly different from each other.

All tests were conducted between 09h00 and 12h00. The apparatus was a petri-dish (diameter, 90 mm) held vertical by a clamp (fastened to the top of the dish) (lower end of dish, 100 mm above table top). There were two holes, one in the centre of each side of the dish. The mount (cork with dead spiders on the narrow end) fit in one of the holes (diameter, 25 mm), the narrow end of the cork being flush with the inside of the dish. A clear plastic tube (diameter, 10 mm) was positioned so that its nearest end was pushed against, and opened into, the other hole (diameter, 10 mm) (i.e., it opened through a hole directly opposite the mount). A clamp (connected to a stand) held the tube in place, and the far end of the tube was plugged by a cork.

Testing was initiated by removing the cork from the distal end of the tube, putting a test spider (a juvenile of *P. africana*) in the tube from this end, and then replacing the cork. Tests began when the test spider walked out of the tube and entered the cage. Tests were aborted if the test spider leapt, instead of walking, out of the tube or if it did not leave the tube within 30 min. Aborted tests were rare.

For successful tests, one of four outcomes was recorded: the test spider ‘settled’ (definition: the test spider walked on to the mount and became quiescent for 5 min, but without first touching one of the dead spiders or the silk over a spider); ‘attacked’ (the test spider leapt or lunged at, and contacted, one of the dead spiders or the silk over a dead spider); ‘walked over’ (without leaping or lunging first, the test spider stepped on to a dead spider or the silk); ‘no response’ (60 min elapsed without the test spider settling, attacking or walking over). Walking over was an uncommon outcome (never more than 5% of the 100 replicates for any given scene), and statistical findings always refer ‘settle versus did not settle’ or ‘attack versus did not attack’.

During encounters with living oecobiids, *Portia* usually adopted a particular orientation (facing directly toward the oecobiid in the nest), although other orientations were occasionally seen. Here the expression ‘typical orientation’ is used whenever the test spider, when settled, was oriented no more than 45° away from straight toward a mount made from a dead spider or a nest. Any other orientation is recorded as ‘atypical orientation’.

The scene was arranged centred on the cork (i.e., the centre of the array of spiders and nest was at the centre of the cork, directly across from the centre of the hole through which the test spider entered the dish). When only a single dead spider was present, it always faced downward. Any spider in a nest faced downward unless stated otherwise. When a scene included a nest and also a mounted spider outside the nest, the nearest part of the spider’s body and the nearest edge of the nest were c. 2 mm apart. When two or three mounted spiders were arranged around a nest, each was c. 2 mm away from the nest. However, when there were more than one

mounted spiders lined up one behind the other and outside the nest, the second was 2 mm from the first and, if there were a third, the third was 2 mm from the second.

RESULTS

Scenes made with mounts elicited behaviour that had previously been seen with living oecobiids and *P. africana*, providing a basis for addressing a series of questions.

Are the test spider's decisions influenced by whether an oecobiid is in a nest or not?

There was no significant difference in how often *Portia* attacked oecobiids that were in nests versus oecobiids that were not in nests (Table 4.1. Rows 1 & 2) ($\chi^2=1.41$, $P=0.2348$). However, *Portia* more often settled with the oecobiid that was in a nest than with the oecobiid that was not in a nest ($\chi^2=11.61$, $P=0.0007$) (31 of 36 adopted typical orientation with the oecobiid inside a nest and 9 of 15 adopted typical orientation with oecobiids in the absence of nests).

Does whether a solitary spider in a scene is an oecobiid or another *Portia* influence the test spider's decisions?

When there was no nest present (Table 4.1. Rows 2 & 4), *Portia* attacked ($\chi^2=11.97$, $P=0.0005$) and settled ($\chi^2=10.86$, $P=0.0010$) significantly more often when there was a solitary *Oecobius* in the scene instead of a solitary *Portia*. *Portia* also attacked ($\chi^2=12.77$, $P=0.0004$) and settled ($\chi^2=40.62$, $P<0.001$) more often when the solitary spider was in a nest was *Oecobius* instead of *Portia* (Table 4.1. Rows 1 & 3). In fact, the test spider never attacked the *Portia* in the nest. One test spider adopted typical orientation with a *Portia* that was without a nest. The other two test spiders adopted atypical orientation when they settled with *P. africana* juveniles.

Does seeing another *Portia* settled at a nest, with an oecobiid inside, influence the test spider's decisions?

How often *Portia* attacked when there was another *Portia* settled at a nest (Table 4.1. Row 5) was not significantly different from how often *Portia* attacked when there was no other *Portia* at a nest (Table 4.1. Row 1) with an *Oecobius* ($\chi^2=0.89$, $P=0.3458$). All attacks were on the nest, not on the *Portia* settled beside the nest. However, *Portia* settled more often when there was another *Portia* was with the *Oecobius* (51 of 59 in typical orientation) and less often when the *Oecobius* was alone ($\chi^2=10.61$, $P=0.0011$).

When there are two mounted spiders in the scene (one *Portia* and one *Oecobius*), with one in a nest and other settled outside, are the test spider's decisions influenced by the identity of the spider in the nest?

The number of attacks when the spider in the nest was *Oecobius* (Table 4.1. Row 5) was not significantly different from the number of attacks when the spider in the nest was *Portia* (Table 4.1. Row 6) ($\chi^2=1.96$, $P=0.1612$). Almost all attacks were aimed at the oecobiid, regardless of whether the oecobiid was the spider inside or outside the nest (100% when oecobiid was inside and 13 out of 15 when *Portia* was inside). *Portia* settled when the spider in the nest was *Oecobius* much more often than when the spider in the nest was *Portia* ($\chi^2=67.00$, $P<0.001$). When a *Portia* was in the nest, only two of the five test spiders that settled that adopted typical orientation.

When there is a *Portia* already settled at a nest, with an oecobiid inside, are the test spider's decisions influenced by whether the settled *Portia* is facing toward or away from the oecobiid?

The number of attacks when *Portia* was facing toward the nest (Table 4.1. Row 5) was not significantly different from the number of attacks when *Portia* was facing away from the nest (Table 4.1. Row 7) ($\chi^2=0.06$, $P=0.7998$). In the scene with *Portia* facing away, one of the attacks was aimed at the *Portia* instead of the nest. Test spiders settled when *Portia* was facing the nest

significantly more often than when *Portia* faced away from the nest ($\chi^2=15.84$, $P=0.0001$) (27 of 31 test spiders adopted typical orientation when *Portia* faced away from the oecobiid).

When there are two spiders in the scene, one in a nest and other settled outside, are the test spider's decisions influenced by seeing specifically that the spider inside is an oecobiid and the spider outside is *Portia*?

When both mounted spiders were oecobiids (Table 4.1. Row 8), how often the test spider attacked was not significantly different from how often it attacked when the scene was a *Portia* settled with *Oecobius* inside the nest (Table 4.1. Row 5) ($\chi^2=5.18$, $P=0.0228$, NS with Bonferroni adjustment). The test spider aimed its attack at the oecobiid in the nest in 16 instances and at the oecobiid outside in three. Test spiders settled less often when both mounted spiders were *Oecobius* than when the scene was *Portia* outside and *Oecobius* inside ($\chi^2=53.13$, $P<0.001$). Nine of ten test spiders adopted typical orientation when with two oecobiids, with six oriented toward the oecobiid that was inside the nest and three oriented toward the oecobiid that was outside the nest.

When both mounted spiders were *Portia* (Table 4.1. Row 9), the test spider rarely attacked or settled. Only one attack was seen, and it was aimed at the *Portia* settled outside the nest. The number of times the test spider attacked when the scene was two *Portia* was not significantly different from when the scene was a *Portia* and an oecobiid (Table 4.1. Row 5) ($\chi^2=5.70$, $P=0.0170$, NS with Bonferroni adjustment). The number of test spiders that settled when the scene was two *Portia* was significantly less than the number that settled when the scene was a *Portia* and an oecobiid ($\chi^2=67.00$, $P<0.001$). When with two *Portia*, four out of five test spiders adopted typical orientation (oriented toward the *Portia* that was inside a nest).

At a nest, with the oecobiid inside, are the test spider's decisions influenced by whether a single *Portia* is settled with an oecobiid or two *Portia* are settled at opposite ends of the nest?

The number of attacks when only one *Portia* was present (Table 4.1. Row 5) was not significantly different from the number of attacks when two *Portia* were present (Table 4.1. Row 10) ($\chi^2=0.07$, $P=0.7883$). All attacks were aimed at the nest when only one *Portia* was settled outside. However, when two *Portia* were present, all attacks were aimed at one of the two *Portia*, not at the nest. Significantly more test spiders settled when there was one instead of two *Portia* in the scene ($\chi^2=30.08$, $P<0.001$). When there were two *Portia* already settled at a nest, all test spiders adopted typical orientation. Although most (18 of 21) were oriented toward the nest, three were oriented toward one of the two *Portia*.

When two *Portia* are settled with an oecobiid (in a nest), are the test spider's decisions influenced by whether the two *Portia* are at opposite ends of the nest or lined up at one end?

The number of attacks by test spiders when two *Portia* were settled one at each end of the nest (with *Oecoibius* inside) (Table 4.1. Row 10) was not significantly different from the number that attacked when the two *Portia* were lined up on the same side of the nest (Table 4.1. Row 11) ($\chi^2=1.68$, $P=0.1944$). With the two *Portia* lined up on the same side of the nest, one attack was aimed at the nest, but the other two were aimed at one of the two *Portia*. The number of test spiders that settled with two *Portia* lined up on one side (24 of 26 adopted typical orientation) was also not significantly different from the number that settled with two *Portia* at opposite ends of a nest ($\chi^2=0.70$, $P=0.4044$).

Are the test spider's decisions influenced by whether there are two or three *Portia* settled around a nest with an oecobiid inside?

The number of attacks when two *Portia* were present (one at each end of the nest) (Table 4.1. Row 10) was not significantly different from the number of attacks when three *Portia* were present (Row 12) ($\chi^2=2.91$, $P=0.0881$). With three *Portia* settled around the nest, each attack was aimed at one of the *Portia*, not at the nest. However, no test spiders settled when there were three instead of two *Portia* settled around the nest, this being significantly less test spiders settling than when two *Portia* were present ($\chi^2=23.46$, $P<0.001$).

When three *Portia* are settled with an oecobiid (in a nest), are the test spider's decisions influenced by whether the three are at positioned around the nest or lined up at one end?

How often test spiders attacked when three *Portia* were settled around the nest (with *Oecobius* inside) (Table 4.1. Row 12) was not significantly different from how often they attacked when the three *Portia* were lined up on the same side of the nest (Table 4.1. Row 13) ($\chi^2=0.69$, $P=0.4071$). With the three *Portia* lined up at one side of the nest, three attacks were aimed at the nest and one was aimed at one the *Portia* that was closest to the nest. Significantly more test spiders settled when three *Portia* were lined up on one side instead of around the nest ($\chi^2=35.29$, $P<0.001$) (27 of 30 adopted typical orientation, 26 toward the oecobiid and one toward one of the *Portia*). The number of test spiders that attacked ($\chi^2=0.15$, $P=0.7004$) and settled with ($\chi^2=0.40$, $P=0.5287$) three *Portia* lined up on one side of a nest (Row 13) was not significantly different from the number that attacked and settled with two *Portia* lined up on one side of a nest (Table 4.1. Row11).

DISCUSSION

Despite the small size of their eyes, *P. africana* juveniles evidently distinguished by sight between two types of spiders, other *P. africana* juveniles and *O. amboseli*. They made these discriminations when the body lengths of the two spiders were similar and there are no cues from movement patterns. Even when the spiders being viewed were covered by silk (simulation of a

nest), *P. africana* juveniles distinguished between *O. amboseli* and *P. africana*. For *P. africana* juveniles, the appropriate target for attacking and especially for settling appears to be the oecobiid, not the other *P. africana* juveniles. Nonetheless, *P. africana* juveniles seem to factor in the presence of other *P. africana* juveniles when making settling decisions.

Settling is a distinctive behaviour pattern in which, instead of attacking immediately, *P. africana* juveniles become quiescent, usually while facing an individual of *O. amboseli* that is inside a nest (i.e., *Portia* waits). After a lengthy pause, the *P. africana* juvenile may lunge at the nest, stimulating the oecobiid to dash away from the nest. As the oecobiid leaves or else when it later returns to the nest, the *P. africana* juvenile may capture it. Or another *P. africana* juvenile may capture the oecobiid and share the meal.

Some of the rules governing the predatory strategy of *P. africana* juveniles during encounters with *O. amboseli* are suggested by the findings from experiments using scenes made from mounted dead spiders and nests. Seeing a solitary *O. amboseli* seems to be a cue for predatory behaviour (attack or settle), while seeing that an oecobiid is inside a nest seems to predispose *P. africana* juveniles toward settling.

Seeing *P. africana* juveniles already settled with an oecobiid is also influential, with settling decisions depending on how the other individuals are situated around the oecobiid's nest and on the number of other *P. africana* that are part of the scene. Deciding whether to settle when others are already present can be called the *P. africana* juvenile's joining decision, and a particular combination of stimuli seems to be especially conducive to joining: seeing one other *P. africana* juvenile settled with an oecobiid in a nest, with the settled *P. africana* juvenile being in the typical settling orientation (facing the oecobiid).

When the settled *P. africana* juvenile was facing away from the oecobiid, there was less joining. Perhaps a living *P. africana* that is not in the typical orientation is typically inattentive to the prey, and therefore not prepared to capture it. From a potential joiner's perspective, an

inattentive partner may be of little assistance. It might, in fact, be an active problem, should it choose to interact with the joiner.

Sometimes *P. africana* aimed its attack at another *P. africana* juvenile instead of at the oecobiid. The functional significance of these attacks is uncertain. Perhaps these attacks were cases of mistaken identification, with a *P. africana* juvenile misidentifying another *P. africana* as an oecobiid, or perhaps there was no mistaken identification and instead these were instances of the *P. africana* having decided to prey on a conspecific individual. An alternative is that these attacks were not predatory and were instead instances of the test spider attempting to drive away a rival.

‘Go for more’ does not accurately describe the decisions made by *P. africana* juveniles. *P. africana* juveniles apparently decide to join specifically on the basis of seeing one other *P. africana* juvenile settled with an oecobiid. Seeing an oecobiid in a nest with another oecobiid settled by the nest is not especially conducive to joining, nor is seeing a *P. africana* juvenile settled by a nest with another *P. africana* juvenile inside the nest. Apparently, the spider inside the nest needs to be specifically the oecobiid and the spider settled outside the nest needs to be specifically the *P. africana* juvenile.

Potential joiners are apparently influenced by numbers, and it is specifically the number (one or two) of other conspecific juveniles already present in the scene that seems to matter. When more than one *P. africana* juvenile is present, only one individual will potentially capture the oecobiid. More than one individual sometimes feed together, but attempts to join as a feeder are resisted by the successful *P. africana* juvenile. There are also geometrical constraints. With the prey, an adult *O. amboseli*, being similar in size to another *P. africana* juvenile, there is limited space for fitting more than one other *P. africana* juvenile around the prey. For *P. africana* juveniles, the payoff from joining may tend to be low when more than one other *P. africana* juvenile is already settled with an oecobiid. The risk of going hungry may favour a policy of joining when there is no more than one other *P. africana* juvenile is already settled

with an oecobiid. Making this choice does not require that the individual *P. africana* juvenile weighs the odds and makes a decision on the basis of having calculated the risks. The individual *P. africana* juvenile might be programmed with a simple rule: do not join when more than one other *P. africana* juvenile is settled with the oecobiid. Nonetheless, this rule is interesting because of an apparent requirement that the individual *P. africana* juvenile has at least a rudimentary perception of the difference between one and more than one items of a particular kind (i.e., other *P. africana* juveniles).

However, finding that there was less joining when two, instead of one, other *P. africana* juveniles were already with the oecobiid does not suffice to show that it was the number of *P. africana* juveniles that influenced the potential joiner's decision. When one *P. africana* juvenile is at one side of a nest and another is at the other side, *P. africana* juveniles may detect that there is not a lot of room left over for a third *P. africana* juvenile to find a place to settle at the nest (crowded-space hypothesis). However, this hypothesis alone does not explain all of the experimental findings. Even when both of the two already settled *P. africana* juveniles were lined up on one side of the nest (i.e., with the crowding of space alongside the nest thereby being comparable to what it is with only one *P. africana* juvenile already settled), the test joined no more often than when the two *P. africana* juvenile already present were at the two ends of the nest. The number (two) appears to be the variable that matters (for *P. africana* juveniles, two is a crowd).

When there are already three other *P. africana* juveniles spaced around an oecobiid, no joining was recorded in experiments using mounts, consistent with not seeing this in nature. It is tempting to suggest that the *P. africana* juvenile sees there are three, not two, other *P. africana* juveniles already present and that *P. africana* juveniles are programmed not to join when they see three other *P. africana* juveniles already present because this is clearly a losing proposition. However, the experimental findings suggest a somewhat different explanation. The crowded-space hypothesis applies with even more force when there are three instead of only two *P.*

africana juveniles spaced around an oecobiid nest. However, when the three already settled *P. africana* juveniles were lined up at one side of the nest, the space at the nest for a joiner was the same as when only one already-settled *P. africana* juvenile is there and the same as when two *P. africana* juveniles are lined up on one side of a nest. The number of *P. africana* juveniles that joined was higher when the three already-settled *P. africana* juveniles were on one side than when they were spaced evenly around the nest, but not distinguishably different from the number that joined when it was two, instead of three, *P. africana* juvenile lined up at one side.

P. africana juveniles seem to distinguish between one and more than one *P. africana* juveniles already settled, but there is no evidence that they distinguish between two and three. Nor is there any clear reason why they should. The odds of sharing a meal may drop off so drastically when the number of *P. africana* juveniles already present goes from one to two that making additional distinctions, in the context of this particular predatory tactic, between larger numbers than one and two may be trivial.









Spider feeding mechanics may compound the problem of limited space at the prey. Perhaps a lion pride or a wolf pack is not a good analogy for a group of feeding spiders. When quarrelling over the carcass of a zebra, a lion may rip off a hunk of meat to carry away to eat in peace. Spiders are different. Instead of chewing, they feed by extra-oral digestion (Cohen 1995, 1998). Enzymes are injected into the prey, and left while they liquefy prey tissue, then the liquid meal is sucked in by the spider (Pollard 1990). This process is repeated many times in a feeding bout (Pollard 1989). When *P. africana* juveniles join, they do not have the option of running off with a piece of an oecobiid carcass. Normally they succeed only if they can establish themselves at a secure position on the oecobiid carcass and remain there, more or less unmolested by neighbours, for long enough to feed by extra-oral digestion. A crowd of aggressive *P. africana* juveniles does not seem compatible with these requirements, and one feeding neighbour may be as many as are conducive to communal feeding by *P. africana* juveniles.




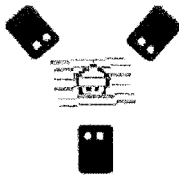

This is a hypothetical adaptive explanation for why *P. africana* juveniles stop counting after they reach two. There is an alternative hypothesis that would make this adaptive explanation irrelevant. Perhaps counting beyond two is simply beyond the cognitive ability of these small spiders with their small eyes and their small brains. Being something like a null hypothesis, this capacity-limits hypothesis may not be easy to test.

P. africana juveniles seem to count accurately only up to two, and this may not appear very impressive. However, much bigger vertebrates such as salamanders may not count accurately beyond three (Uller *et al.* 2003). It is difficult to draw conclusions about phylogenetic trends in ability related to numerosity and ordinality because most experimental studies designed specifically to investigate these particular cognitive abilities have been conducted on vertebrates and especially on primates (Hauser *et al.* 2000, Rumbaugh and Washburn 1993).

Besides having considered an arthropod instead of a vertebrate, the experiments using *P. africana* are unusual in another way. Instead of a go-for-more rule, *P. africana*'s rule during encounters with oecobiid-*Portia* combinations seems to be to choose a particular optimum number. Moreover, the identity of the spiders being counted and their positioning appear to be attended to by the decision-making *P. africana* juvenile.

Table 4.1. Data from testing *Portia africana* juveniles with ‘scenes’ made from mounting dead spiders and nests on cork positioned inside Petri dish. Test spider enters dish from opposite side. See text for details. N=100 for each scene. Number of test spiders that attacked and number that settled indicated. Pentagon: oecobiid. Rectangle: *P. africana* juvenile. Wavy lines: nest.

Scene	Attacked	Settled	Diagram
1. One <i>Oecobius</i> . Covered by silk	12	36	
2. One <i>Oecobius</i> . No silk	18	15	
3. One <i>Portia</i> . Covered by silk	0	1	
4. One <i>Portia</i> . No silk	3	2	
5. One <i>Oecobius</i> & one <i>Portia</i> . <i>Oecobius</i> covered by silk. Facing each other.	8	59	
6. One <i>Oecobius</i> & one <i>Portia</i> . <i>Portia</i> covered by silk. Facing each other.	15	5	
7. One <i>Oecobius</i> & one <i>Portia</i> . <i>Oecobius</i> covered by silk. <i>Portia</i> & <i>Oecobius</i> facing in opposite directions (i.e., <i>Portia</i> facing out from nest).	9	31	
8. Two <i>Oecobius</i> . One <i>Oecobius</i> covered by silk. Facing each other.	19	10	

9. Two <i>Portia</i> . One <i>Portia</i> covered by silk. Facing each other.	1	5	
10. One <i>Oecobius</i> & two <i>Portia</i> . <i>Oecobius</i> covered by silk. <i>Oecobius</i> & one <i>Portia</i> facing each other. Other <i>Portia</i> facing rear of <i>Oecobius</i> . The two <i>Portia</i> at opposite ends of the nest.	7	21	
11. One <i>Oecobius</i> & two <i>Portia</i> . <i>Oecobius</i> covered by silk. <i>Oecobius</i> & 1 st <i>Portia</i> facing each other. 2 nd <i>Portia</i> directly behind, & facing rear of, 1 st <i>Portia</i> .	3	26	
12. Three <i>Portia</i> and one <i>Oecobius</i> . <i>Oecobius</i> covered by silk. Three <i>Portia</i> in triangle. All <i>Portia</i> facing inward. <i>Oecobius</i> at centre of triangle, facing one of the <i>Portia</i> .	2	0	
13. Three <i>Portia</i> and one <i>Oecobius</i> . <i>Oecobius</i> covered by silk. <i>Oecobius</i> & 1 st <i>Portia</i> facing each other. 2 nd <i>Portia</i> directly behind, & facing rear of, 1 st <i>Portia</i> & 3 rd <i>Portia</i> directly behind, & facing rear of, 2 nd .	4	30	

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A new species of *Myrmarachne* from Kenya (Araneae: Salticidae)

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ABSTRACT. Description of *Myrmarachne melanotarsa* n. sp., an ant-like jumping spider from eastern Africa is given. This species, mimicking *Crematogaster* ants, is the first social *Myrmarachne* species hitherto known.

Key words: arachnology, Araneae, Salticidae, *Myrmarachne*, new species, Afrotropical Region, ant mimicry, sociality.

Myrmarachne MACLEAY, 1838 is a very large genus of strongly sexually dimorphic ant-like salticids. Ants may be particularly suitable models because they are avoided by many potential predators of spiders. In most instances, the resemblance of *Myrmarachne* species to ants appears to be an example of Batesian mimicry. Ant mimicry may limit variation range of the general morphology within the genus. However, even genital organs, especially of males, appear to be remarkably similar in all *Myrmarachne* species.

The hitherto known 58 Afrotropical species of the genus were revised by WANLESS (1978). Using details of the copulatory structures he recognized several species-groups in this region. A new species from the *tristis* species-group, found in Kenya is described below. This spider is the first social *Myrmarachne* species.

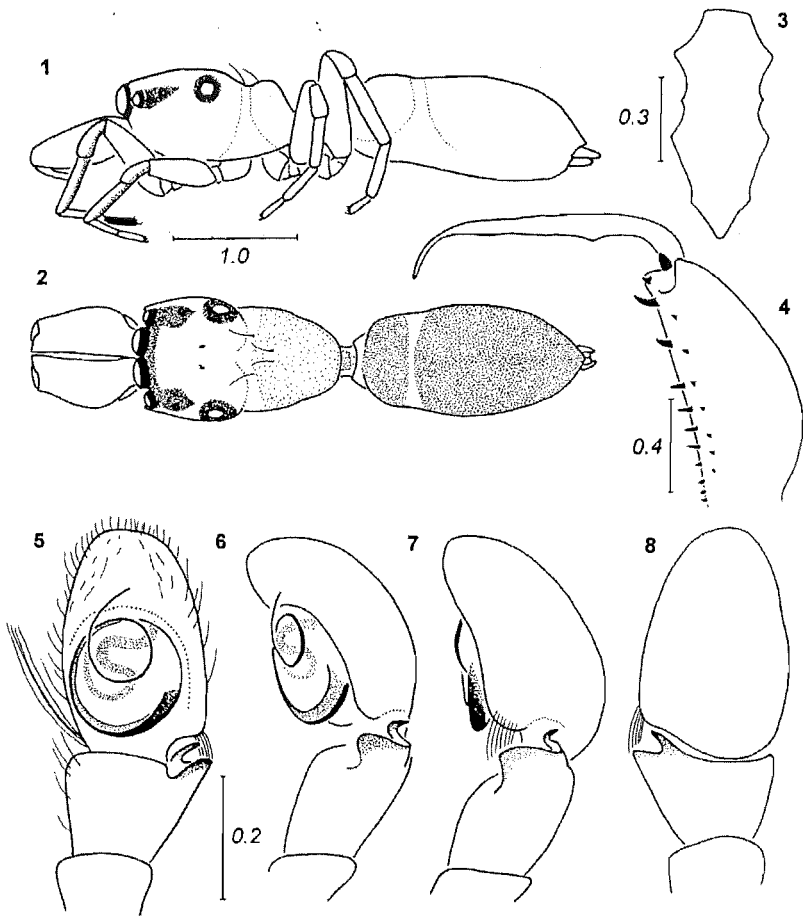
Myrmarachne melanotarsa n. sp.
(Figs 1-16)

ETYMOLOGY

The specific name refers to the black tarsi of the first legs.

DIAGNOSIS

This species is closely related to *Myrmarachne luachimo* WANLESS, 1978 from Angola. *M. melanotarsa* differs from it in the black first tarsi and sparser spination

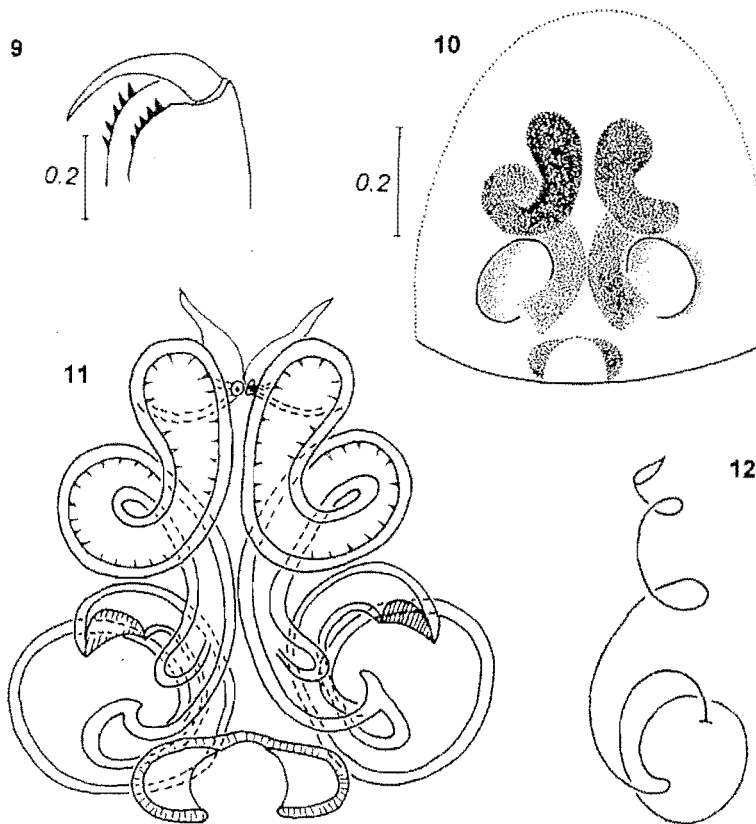


1-8. *Myrmarachne melanotarsa* n. sp., male, paratype: 1-2 – general appearance, lateral and dorsal views, 3 – cheliceral dentition 4 – sternum, 5-8 – palpal organ ventral, ventrolateral, lateral and dorsal views

of first tibiae. The male may be distinguished by details of the pedipalp structure; a hooked tibial apophysis (sigmoid in *M. luachimo*), very well developed flange of the apophysis and narrower membraneous pars pendula along basal part of the embolus (cf. Figs 5-7 and Figs 15 B, 15 H in WANLESS 1978). The female has simpler spermathecae forming only one loop, while in *M. luachimo* spermathecae are convoluted and form an "eight" figure (cf. Fig. 11 and Figs 15 D, 15 E in WANLESS 1978).

DESCRIPTION

Measurements [in mm] (male/female). Carapace length 1.5-1.8/1.5-1.7, width 0.9-1.0/0.8-1.0, height 0.5-0.6/0.4-0.6. Abdomen length 1.6-2.1/1.8-2.2, width 0.8-1.1/0.8-1.2. Eye field length 0.7-0.8/0.6-0.7, anterior width 0.7-0.9/0.7-0.8, posterior width 0.8-1.0/0.8-0.9.

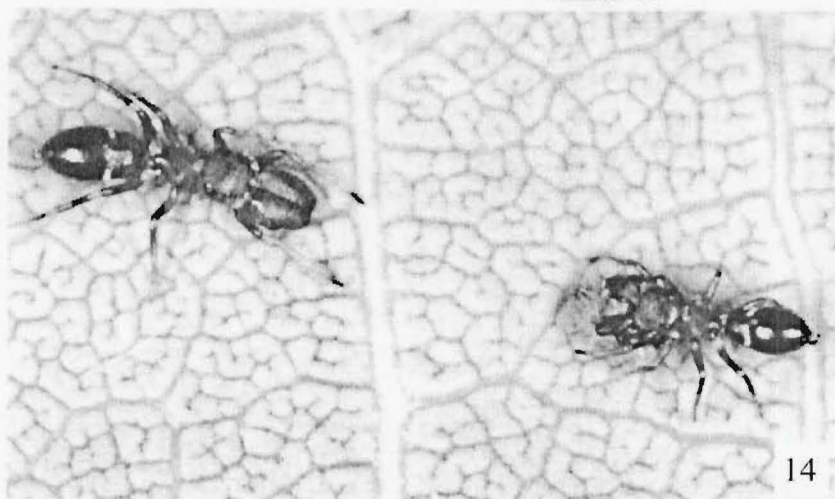


9-12. *Myrmarachne melanotarsa* n. sp., female, paratype: 9 - cheliceral dentition, 10 - epigyne, 11 - internal structure of epigyne, 12 - diagrammatic course of seminal duct

Male. Small ant-like spider, general appearance as in Figs 1-2. Carapace constricted with distinct thoracic "hump". Coloration of carapace light brown or brownish red, eyes surrounded by black rings. Eye field punctured reticulate, with numerous silver spots of internal guanine crystals. Long thin brown hairs on

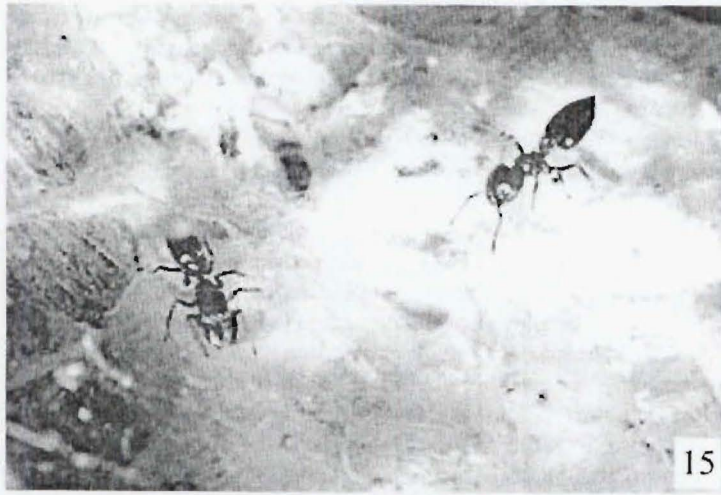


13



14

13-14. *Myrmarachne melanotarsa*: 13 - eating a small salticid, 14 - on a leaf



15. *Myrmarachne melanotarsa* (left) with its model, *Crematogaster* sp. ant (right); 16. *Myrmarachne melanotarsa* on a communal silk sheet

carapace, wedge-shaped patches of whitish hairs on lateral surfaces of carapace, in postocular constriction. Pair of long trichobothria in constriction furrow, second pair on thoracic "hump" (Fig. 2). Chelicerae reddish orange, with 9-11 promarginal teeth and 5-7 on retromargin, fang with small bump-shaped apophysis (Fig. 3). Clypeus very low. Labium and maxillae light brown. Sternum brown, its shape as in Fig. 4. Pedicel short. Abdomen ovoid, slightly elongated, greyish beige to blackish, with two scuta separated by lighter transverse band formed by white hairs. Venter dark, greyish brown. Spinnerets grey. Coxae and trochanters brownish orange, only trochanter IV very light, yellowish white. Legs I and II brownish orange, darker stripes along lateral surfaces of their patellae and tibiae. Tarsi of first legs black. Legs III and IV light brown with slightly lighter metatarsi and tarsi, patella IV light basally. Ventral spination of legs I: tibiae 0 or 2, metatarsi 0-2 or 2-2. Pedipalps brown. Tibial apophysis short, hooked, with well developed flange, protected by depression in cymbium and tuft of long bristles on proximal ectal edge of cymbium (Figs 6-7). Bulbus rounded; tegulum swollen; embolus long and slender, with membranous expansion along its basal half, coiled around bulbus and forming small loop on anterior part of tegulum (Figs 5-6).

Female. Like male. Carapace reddish orange, thoracic "hump" less as in male. Chelicerae with five tooth on both margins (Fig. 9). Abdomen slightly bigger than in male, without scuta, light brown tinged with grey. Book-lung covers big, strongly sclerotized. Coxae I and II yellow, III light brown, IV yellowish with dark ring distally. Leg coloration as in male, first tarsi blackish. Ventral spination of legs I: tibiae 0 or 2, metatarsi 2-2. Pedipalps brown. Epigyne rather weakly sclerotized, with paired pouches at its posterior edge and two rounded depressions (Fig. 10). Initial part of seminal ducts very weakly sclerotized, coiled and widening to large chamber; posterior part strongly sclerotized; spermathecae rather simple (Fig. 11).

TYPE MATERIAL

Holotype: male, Kenya, Mbita Point, 0°25'S 34°13'E, E shore of Lake Victoria, 1150 m a.s.l., February 1998, leg. R. JACKSON (Florida State Collection of Arthropods, Gainesville).

Paratypes: together with holotype, 3 males, 3 females (Florida State Collection of Arthropods, Gainesville); same locality, 1 male, January 1998 (Florida State Collection of Arthropods, Gainesville); same locality as holotype, 2 males, 3 females, May 2001, leg. K. SALM & R. JACKSON (Natural History Museum, London); 2 males, 3 females, May 2001, leg. K. SALM & R. JACKSON (Musée Royal de l'Afrique Centrale, Tervuren).

REMARK

This species belongs to the *tristis*-group of species (WANLESS 1978), including hitherto 24 species in the Afrotropical region.

HABITAT AND BIOLOGY

M. melanotarsa (Figs 13, 14) was studied in East Africa, in the cambretaceous savannah surrounding Lake Victoria in 2001. *M. melanotarsa* is a social spider. Seventy-four colonies were identified for general study purposes, and five of these were studied in more detail. The detailed study on *M. melanotarsa* biology will be the subject of a separate paper. Only the basic data are provided here.

This species was found on tree trunks or limbs, especially fig trees (*Ficus* sp.). Colonies were based in nest complexes, comprised of a number of adjoining silk retreats unified by a sheet of communal silk (Fig. 16). These nest complexes could vary in size from a couple of centimetres to half a metre in length, and contained anything from a couple to hundreds of spiders in each complex. Most commonly, the colonies studied contained between ten and fifty individuals. Nest complexes housed *Myrmarachne* of both sexes and all ages, and frequently contained a number of other cohabiting species of salticid.

M. melanotarsa was found primarily in colonies built around or in old eggsacs of hersiliid spiders on the tree trunks. Sometimes colonies were associated with eggsacs containing eggs and the female hersiliid was even still present in some cases. Often *M. melanotarsa* was in silk surrounding broken places on the trunks (e.g. scar from a severance of the branch). Occasionally, there were colonies in old lepidopteran cocoons on the trunks or in old wasp nests on the tree boughs.

Crematogaster ants, mimicked by *M. melanotarsa*, were almost always common on the same tree trunks and limbs as this spider species. Frequently these ants were actually in spider colonies, on the silk (Fig. 15).

ACKNOWLEDGEMENTS

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Chapter 6

The natural history of *Myrmarachne melanotarsa*, a social ant-mimicking jumping spider

Abstract

Baseline information is provided on the relationship between an East African myrmecomorphic salticid, *M. melanotarsa*, and its model, the ant *Crematogaster*. Questions raised by this information are considered in later chapters.

INTRODUCTION

Spiders that resemble ants ('ant mimics') and spiders that routinely live in the company of other conspecific spiders ('social spiders') are generally different species, but *Myrmarachne melanotarsa* Weslowska and Salm is an interesting exception (Chapter 5: Weslowska and Salm, 2002). This East African salticid is typically found in the company of other conspecific individuals and in the company of its model, the ant *Crematogaster* sp. (near *C. ferruginea* (Forel, 1890)). As initial steps towards understanding the biology of *M. melanotarsa*, observations from the field and the laboratory are reported in this chapter.

MATERIALS AND METHODS

Adults of *M. melanotarsa* and *Crematogaster* sp. are both c 3 mm in body length. Both are common at Mbita Point, on the shore of Lake Victoria in Kenya. Seventy-five colonies of *M. melanotarsa* were monitored opportunistically for the natural history details provided in this chapter. Three of these colonies were especially large (> 50 individuals of *M. melanotarsa* per colony), and these were observed almost daily over a 4-month period. The term '*M. melanotarsa* colony' is used for nest complexes occupied by *M. melanotarsa* regardless of whether other salticid species were also present.

Observations were at different times during the day, and each observation period lasted 20-120 min. Colonies were also established in the laboratory in large plastic cages. Other salticids (*Pseudicius* spp. and *Menemerus* spp.), the ants (*Crematogaster*), and a large variety of potential prey were maintained in the same cages. These colonies were observed opportunistically, along with the colonies in the field.

OBSERVATIONS

Ant activity in nest complexes

It was routine to see *Crematogaster* on the surface of *M. melanotarsa* nest complexes and, as a rule, larger nest complexes harboured more *Crematogaster*. Sometimes other small (unidentified) ants were present as well, but they were almost always a minority when *M. melanotarsa* was present. However, in a few instances, ants other than *Crematogaster* seemed to take over in nest complexes that had formerly been sites primarily of *Crematogaster* activity, and the numbers of *M. melanotarsa* then declined rapidly as well. Large colonies never persisted in the field for long in the absence of *Crematogaster*.

When seen in a nest complex, *Crematogaster* individuals were usually walking over the silk, and they frequently stopped and pressed their faces into the silk while opening and closing their mandibles. Sometimes *Crematogaster* removed prey remains, the remains of already dead individuals of *M. melanotarsa* and of other salticid species in the nest complexes, shed exoskeletons of the salticids and other detritus that they encountered in the nest-complex silk. The ants sometimes took the detritus to their own nests in holes in the tree.

Sometimes *Crematogaster* individuals were seen with eggs of *M. melanotarsa* or with recently hatched early-instar *M. melanotarsa* in their mandibles, and some of these ants were seen carrying these prey back to their nests. In these instances, the silk around the nests containing the

eggs had been torn loose. The origin of these tears is uncertain, as the ants were never actually seen tearing the silk.

On several occasions, I used forceps to pull silk away from nest complexes. Before tearing the silk, ants were moving in a column adjacent to the nest complex, but the column quickly changed direction and swarmed into the damaged nest complex. The salticids (*M. melanotarsa* and other species) from the damaged and neighbouring parts of the complex stepped aside and remained nearby, all the while keeping away from the ants which carried away exposed eggs and recently hatched juveniles from the nest complex.

Interaction between ants and M. melanotarsa

When seen, *M. melanotarsa* was usually either on the silk of a nest complex or close by. However, *M. melanotarsa* sometimes commuted alongside columns of *Crematogaster* heading away from and back to nest complexes, and these *M. melanotarsa* individuals were often 1 m or more from the nearest nest complex. While traveling alongside ant columns, *M. melanotarsa* appeared to react continually to the nearby ants, actively avoiding contact or confrontation. There were also instances in which individuals of *M. melanotarsa* were on leaves on which there were *Crematogaster* individuals nearby, as well as coccids or other homopterans that feed on sap. These leaves were often distant from the nearest nest complex. Occasionally, while on these leaves, *M. melanotarsa* fed on honeydew from the homopterans (Fig. 6.1).

When at a nest complex, *M. melanotarsa* routinely oriented toward and briefly displayed at conspecific individuals that came close, with males tending to display more persistently than females. Displays included specialised posturing similar to that described for other *Myrmarachne* species (see Jackson 1986). Generally the conspecific displayed back briefly, and then the two spiders moved apart. When *Crematogaster* came near, *M. melanotarsa* usually oriented without displaying. If the ant approached, *M. melanotarsa* usually moved away, but sometimes *M.*

melanotarsa males displayed for a few seconds towards *Crematogaster* in much the same way as toward conspecific males, then backed away and avoided the ant.

Despite *M. melanotarsa*'s apparent efforts to avoid physical contact with *Crematogaster*, face-to-face encounters were frequent. When this happened, *M. melanotarsa* adopted behaviour strikingly similar to how a *Crematogaster* normally reacted when face to face with another *Crematogaster*. *M. melanotarsa*, like *Crematogaster*, cocked its abdomen up almost perpendicular to the substrate and then the spider and the ant 'antennated' each other, the ant with its real antennae and the spider with its antenna-like forelegs. These interactions lasted a few seconds at most, and usually they ended with both individuals departing by moving past each other. Occasionally, when the ant appeared especially agitated and aggressive, with its abdomen pointing almost forward, and *M. melanotarsa* turned and moved rapidly away. *M. melanotarsa* never adopted an abdomen-forward posture comparable to the ant's.

Interactions between M. melanotarsa and other nest-complex residents

The way other salticid species present in the nest complexes reacted to *M. melanotarsa* tended to resemble how they reacted to *Crematogaster*. They paused and oriented towards the ant or its mimic. If the ant or the mimic moved away, the salticid usually watched it (i.e. the salticid maintained orientation towards the ant or mimic) until several body lengths further away. Then the salticid continued on its way. However, if the ant or its mimic approached the salticid, the salticid usually turned and moved quickly away ('ran') or else first backed away a few millimetres before turning and running. *Crematogaster* and *M. melanotarsa*, showed little response to the other salticids. If contact was made, the ants often cocked their abdomens and became agitated, then moved away. If approached by another salticid, there was typically no reaction by *M. melanotarsa* until the other salticid came to within a few body lengths, at which point *M. melanotarsa* turned and ran, typically without turning to reorient toward the salticid.

Prey and predatory behaviour

Most (52 of 71, 73%) prey in the field, being small (evidently c. 1 mm in body length or less) and already considerably masticated when first seen, could not be even tentatively identified. Of the 19 identified prey (Fig 6.2), the majority (68%) was either spider eggs or recently hatched juveniles of spiders, with recently hatched salticids accounting for 37% of the identified prey. Many of the *M. melanotarsa* colonies were built into the eggsacs of a hersiliid spider, *Hersilia caudata*. These eggsacs were common on tree trunks and they were evidently a source of food as well as shelter: hersiliid eggs and juveniles accounted for 17% of the identified prey.

Finding *M. melanotarsa* in the act of feeding on spider eggs and juvenile spiders in the field was difficult because in each instance the *M. melanotarsa* was partly obscured from view by silk. When feeding on a hersiliid (egg or juvenile), *M. melanotarsa* was under the hersiliid eggsac silk. When feeding on a salticid (egg or juvenile), *M. melanotarsa* was under the nest-complex silk. Attempting first to remove the silk always disturbed the feeding *M. melanotarsa*, causing it to drop the prey and run away. Eventually I found a procedure that worked. First I determined by observation through the silk (with a magnifying glass) that the *M. melanotarsa* was indeed feeding, and then I carefully removed the silk, all the while keeping the prey in view. When the *M. melanotarsa* fled, the prey could be retrieved with forceps from the silk. With prey retrieval being so difficult, there were still numerous unconfirmed instances of suspected feeding by *M. melanotarsa* on spiders and their eggs.

Observation of predation on spider eggs and juveniles was easier in the laboratory because silk could be cleared away ahead of time, and laboratory observations confirmed that *M. melanotarsa* readily ate salticid and hersiliid eggs and juveniles. In the laboratory, *M. melanotarsa* also fed on representatives of each of the other prey categories recorded from the field, as well as on aphids, psyllids, whiteflies, mealy bugs, and other unidentified small, soft-bodied insects.

Predatory sequences with insect prey, and with juvenile salticids that were out of the eggsac, began when *M. melanotarsa* oriented from several body lengths away and approached. When close, *M. melanotarsa* lunged ('lunge' is defined by rear legs remaining on the substrate when the spider suddenly moves its body forward) and grabbed hold of the prey. *M. melanotarsa* never leapt on prey ('leap' is defined by all legs leaving the substrate).

M. melanotarsa did not lunge at the eggs and juveniles of spiders encountered inside eggsacs. Instead, *M. melanotarsa* simply took hold of an egg or juvenile with its chelicerae. Next it usually pulled the juvenile spider or egg out of the eggsac to feed. Sometimes eggs, however, were not lifted out, being fed on instead while they remained embedded in the silk. *M. melanotarsa* also preyed on recently hatched juveniles by lunging at them just as they left eggsacs.

M. melanotarsa was never seen to attack adult ants. Nor was it ever seen attempting to feed on the ants' eggs, larvae, and pupae as long as the adult ants were present. However, by simply taking hold with its chelicerae, without first lunging, *M. melanotarsa* readily fed in the laboratory on unguarded eggs, larvae, and pupae of *Crematogaster*.

Mouthing silk

When mouthing silk, *M. melanotarsa* stood with forelegs highly flexed, cephalothorax angled 10-45° downward and the front of the cephalothorax (chelicerae, and sometimes also the clypeus and anterior medial eyes) pressed against the silk. This posture was usually held for only a few seconds, but sometimes it was held for a minute or more. Fangs were inserted into the silk, and sometimes the spider slowly (1-2x per s) opened and closed its chelicerae. Immediately before mouthing, the spider usually probed with its legs 1 (i.e., it moved these two legs forward and backward so that the tarsi pushed alternately on the silk (c. 2 cycles per s; distance moved 0.5-1.0 mm; phasing of the two legs variable, but primarily alternating). The spider finished mouthing by releasing the grip of its fangs on the silk and simply stepping away. However, mouthing normally

occurred in bouts of 10 or more: the spider mouthed, released the silk, stepped, mouthed again in another location, etc. Mouthing was the dominant behaviour of *M. melanotarsa* during field observation.

DISCUSSION

Adaptive advantage of proximity to ants

Sometimes called ‘cocktail ants’ because of the characteristic way they tilt their abdomens up when agitated, *Crematogaster* is a widespread genus from the subfamily Myrmicinae. Colonies of these ants are common in African and Asian arboreal habitats (Davidson and MacKey 1993), being found especially often in dead wood on otherwise living trees (e.g., in a scar or hollow resulting from a branch having been removed). Honeydew from scale insects (coccids) and other sap-feeding homopterans is important as food for *Crematogaster* (Buckley 1987, Gullan 1997), and no other myrmicine ants feed so actively on honeydew. The evolution of *Crematogaster*’s arboreal habits may have been driven by this specialized diet (Sudd and Franks 1987). Besides feeding on honeydew, *Crematogaster* may sometimes get protein and lipids by preying on the coccids themselves (Bailey 1922, 1923; Carroll and Janzen 1973). On the whole, however, the honeydew-making insects appear to benefit from *Crematogaster*’s attention. This is because the ants repel the potential predators and also assist with sanitation by removing excess honeydew (Way 1963). Less is known, however, about how *M. melanotarsa* might benefit from associating with *Crematogaster*.

That *M. melanotarsa* was typically found in close proximity to its model, *Crematogaster*, is more unusual than it might first appear to be. Although the tendency is for the various species in the genus *Myrmarachne* to live in the same general habitat as their models, the mimic and model usually do not occur in especially close physical proximity (Edmunds 1978, Jackson and Willey 1994). The most notable exceptions in the literature have been species that mimic weaver-ants

(*Oecophylla*) (Collart 1941, Matthew 1954, Wanless 1978) and even these species may be less closely associated with the model ant than *M. melanotarsa* is with *Crematogaster*. My observations suggest that there may be especially intricate, but poorly understood, links between the biology of *M. melanotarsa* and *Crematogaster*.

For understanding how close physical proximity to *Crematogaster* advantages *M. melanotarsa*, the conventional Batesian-mimicry hypothesis (predators that avoid attacking ants tend also to avoid attacking the mimic) is clearly relevant. Living in the vicinity of ants might benefit the mimic by ensuring that it tends to encounter predators that have learned to avoid the model. However, this hypothetical advantage appears relevant to *Myrmarachne* species in general, leaving unexplained why *M. melanotarsa* associates unusually closely with its model.

Mixed-species groups with protector species have been described in a number of animal groups, especially mixed-species bird flocks (Burger 1984, Pius and Leburg 1997, Richardson and Bolen 1999), where one species (the ‘protector’) is more effective at driving predators away and other species in the flock benefit by associating with the protector species. This suggests that, by keeping close company with *Crematogaster*, *M. melanotarsa* might be using *Crematogaster* as a protector species. *Crematogaster* routinely attacks its own potential predators, and also drives away the potential predators of the aphids they tend for honeydew. Potential ant and aphid predators may often be potential predators of *M. melanotarsa* as well. The immediate vicinity of *Crematogaster* may be an especially safe haven for *M. melanotarsa*. Perhaps it is widespread in the genus *Myrmarachne* that the ants these salticids mimic provide protector-species benefits in addition to the Batesian-mimicry benefit, and this may be a rewarding area for future research on *Myrmarachne* species in general, as well as on other ant mimics. However, with this hypothesis, as with the conventional Batesian mimicry hypothesis, there is no obvious explanation for why *M. melanotarsa*, compared with other myrmecomorphic salticid species, associates unusually closely with its model.

Collective Mimicry

In *Myrmarachne*, Batesian mimicry is typically envisaged as individual ant mimics benefiting from their resemblance to individual ants. However, by living in groups, *M. melanotarsa* may have taken ant mimicry a step further. Ants are social insects, and potential predators may often encounter groups of ants rather than encountering ants one at a time. Group size and other characteristics vary between species of ants. However, *Crematogaster* in the field, whether at a nest or travelling along a trail, is almost never found alone. If one *Crematogaster* is attacked, a swarm of other conspecific individuals in the immediate area come to its defense and ward off the predator. Perhaps there are times when one ant does not pose a significant threat to a predator, but a swarm of ants tends to be a bigger problem. Just seeing a large group of ants may be enough to deter many predators. This argument suggests what I call the ‘collective mimicry hypothesis’: a group of *M. melanotarsa* spiders may resemble a swarm of *Crematogaster*.

The collective mimicry hypothesis may account for *M. melanotarsa*’s tendency to maintain especially close physical proximity to its model. For people, and presumably for some of *M. melanotarsa*’s natural predators, a mixed-group consisting of *M. melanotarsa* and *Crematogaster* is hard to distinguish from a pure group of *Crematogaster*, suggesting that, for an individual of *M. melanotarsa*, the prime objective is to be close to other similar individuals. Whether the other individuals are conspecifics or the model may be relatively unimportant. The idea of collective mimicry is investigated further in Chapter 9.

Tolerance of Myrmarachne by it's model, Crematogaster

Whatever the advantages might be for *M. melanotarsa*, living in close proximity to *Crematogaster* presumably requires the ability to divert ant aggression. Ants within a single colony

face a comparable problem: colony coherence depends on inhibition of aggression between members of a colony. In ants, colony recognition is generally mediated by a chemical signature derived from cuticular hydrocarbons (Howard and Blomquist 1982, Fletcher and Michener 1987, Thomas *et al.* 1999, Lahav *et al.* 1999). Recent research on *Cosmophasis bitaeniata* (Allen and Elgar 2001), an Australian salticid, suggests a hypothesis that might apply to *M. melanotarsa*. By mimicking the chemical signature of weaver ants, *Oecophylla smaragdinia*, *C. bitaeniata* masquerades as an ant when it enters the nests of the weaver ants and feeds on the ant's larvae. With *Crematogaster* and *M. melanotarsa*, perhaps there is a similar system of chemical mimicry, but with the function for *M. melanotarsa* being to facilitate the use of ants for protection against predators instead of for facilitating feeding on the ant's larvae.

The potential role of ants as nest cleaners

The concentration of nests in salticid nest complexes may lead to a build up of waste and prey remains, which in turn may encourage deleterious build up of parasites and pathogens. Having observed *Crematogaster* workers collecting prey remains, dead spiders, and other detritus in the colony silk and carrying these items back to their own nests suggests that clean nest complexes might be one of the benefits *M. melanotarsa* gains from *Crematogaster*'s company. Waste disposal may also be a serious problem for social web-building spiders, and for many other animals that live in large fixed colonies. Social web-building spiders devote considerable time to cleaning their communal webs (Buskirk 1981, Tietjen 1986), but *M. melanotarsa* may rely on ants for much of their housekeeping.

Soliciting ants for protection

Web-spinners (Embiopoda) are insects that resemble social salticids by using silk to spin communal oviposition and resting shelters. Ants are common in the same environments as web-spinners, often having trails directly over the silk (Denis 1949, Edgerly 1988). As long as the silk walls are intact, the ants remain outside. However, should the silk covering be breached, ants swarm over the colony, entering through the breach and attacking the inhabitants (Edgerly 1988). This is similar to the reaction of *Crematogaster* to damaged *M. melanotarsa* nest complexes. The ants swarmed over the silk surface of *M. melanotarsa*'s nest complex and into normally inaccessible interior parts of the colony. Once inside, the ant's behaviour changed from foraging as scavengers to aggressive predatory foraging.

First impressions were that the ant had turned on its mimic, with the consequences being unambiguously to the ant-mimic's detriment. However, other possibilities should be considered. Perhaps the swarming ants actually help the spiders.

Perhaps, when the nest complex is under attack, *M. melanotarsa* actually encourages *Crematogaster* to swarm into the breach. This might benefit *M. melanotarsa* because a swarm of *Crematogaster* may then drive predators away before they inflict additional damage on the colony by preying on the exposed eggs and juveniles. Perhaps spiders in the nest complex emit chemical stimuli that mimic *Crematogaster*'s alarm pheromone and pay for *Crematogaster*'s services by letting *Crematogaster* eat part of the brood. This arrangement would work to *M. melanotarsa*'s advantage if the other predators are likely to do more harm than *Crematogaster*.

Using ant trails and feeding on honeydew

Crematogaster generally moves from place to place in columns, and sometimes *M. melanotarsa* joined the marching ants. *Crematogaster* columns often led to honeydew-producing coccids. *M. melanotarsa*, along with *Crematogaster*, fed on honeydew. Feeding on honeydew may be unusual for a salticid, but many examples of something somewhat similar, salticids that feed on nectar from flowers and extra-floral nectaries have been reported (Ruhren and Handel 1999, Pollard *et al.* 1995, Jackson *et al.* 2001) and at least one other species in the genus *Myrmarachne*, *M. foenisex*, has been reported to feed on coccid honeydew (Collart 1929a, Collart 1929b). Perhaps feeding on honeydew is disproportionately common in ant-like salticids, as honeydew-producing insects tend to attract ants and ants would presumably deter most other salticids.

Mouth-pressing behaviour by *Crematogaster* and *M. melanotarsa* has the appearance of feeding. Perhaps honeydew collects on the silk and is subsequently eaten by the ants and spiders. This hypothesis is considered in Chapter 8.

Mixed-species spider groups

M. melanotarsa is distinctive not only for living in close proximity to ants but also for sharing nest complexes with other salticids, especially *Menemerus* spp. and *Pseudicius* spp., and for building nest complexes on and within eggsacs of *H. caudata*. Laboratory observations showed that the eggs and the smallest juvenile stages of salticids and hersiliids are vulnerable to *M. melanotarsa*, and prey records suggest that araneophagy is important in nature. Perhaps the other spiders in mixed-species complexes are often significant to *M. melanotarsa* not only as neighbours but also as food.

At first sight, it might appear maladaptive for other salticids, such as *Menemerus* spp. and *Pseudicius* spp., to share nest complexes with *M. melanotarsa*, a potential predator of eggs and

small juveniles. However, there may be compensating advantages for the other salticids because *M. melanotarsa*, along with *Crematogaster*, may be protector species that effectively wards off salticid predators. *Crematogaster* may attack and actually drive away predators, and both *Crematogaster* (the model) and *M. melanotarsa* (the mimic) may deter predators that are reluctant to approach the ants. For *Menemerus* spp. and *Pseudicius* spp., *M. melanotarsa* may be useful as a protector species indirectly because predators mistake it for *Crematogaster*.

Conclusion

The relationships between *M. melanotarsa*, other salticids, and *Crematogaster* may be the product of a complex interplay of conflicts and benefits. The weighting of these costs and benefits at any one time may determine how we view the relationships between the different participants. Any simple characterisation of how each species is adapted to the other appears unrealistic.

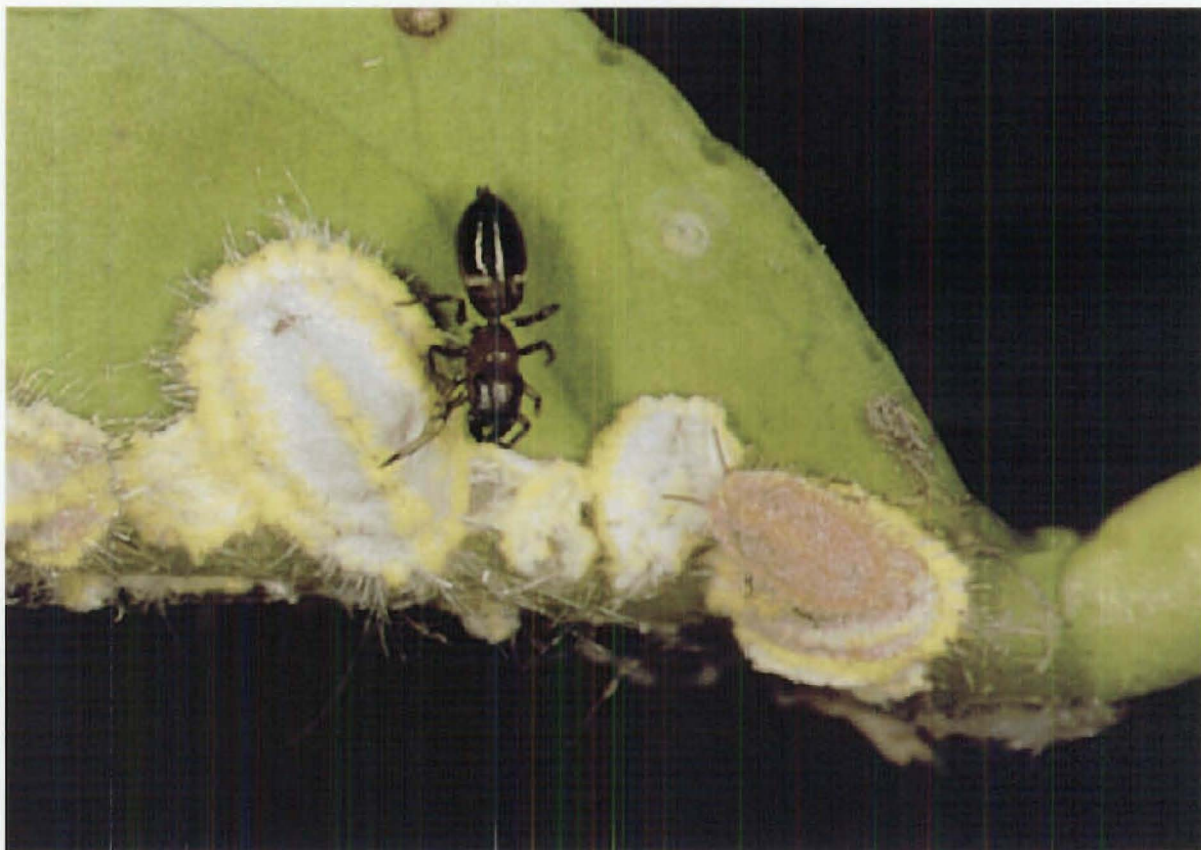


Fig 6.1. *Myrmarachne melanotarsa* with honeydew-producing coccids

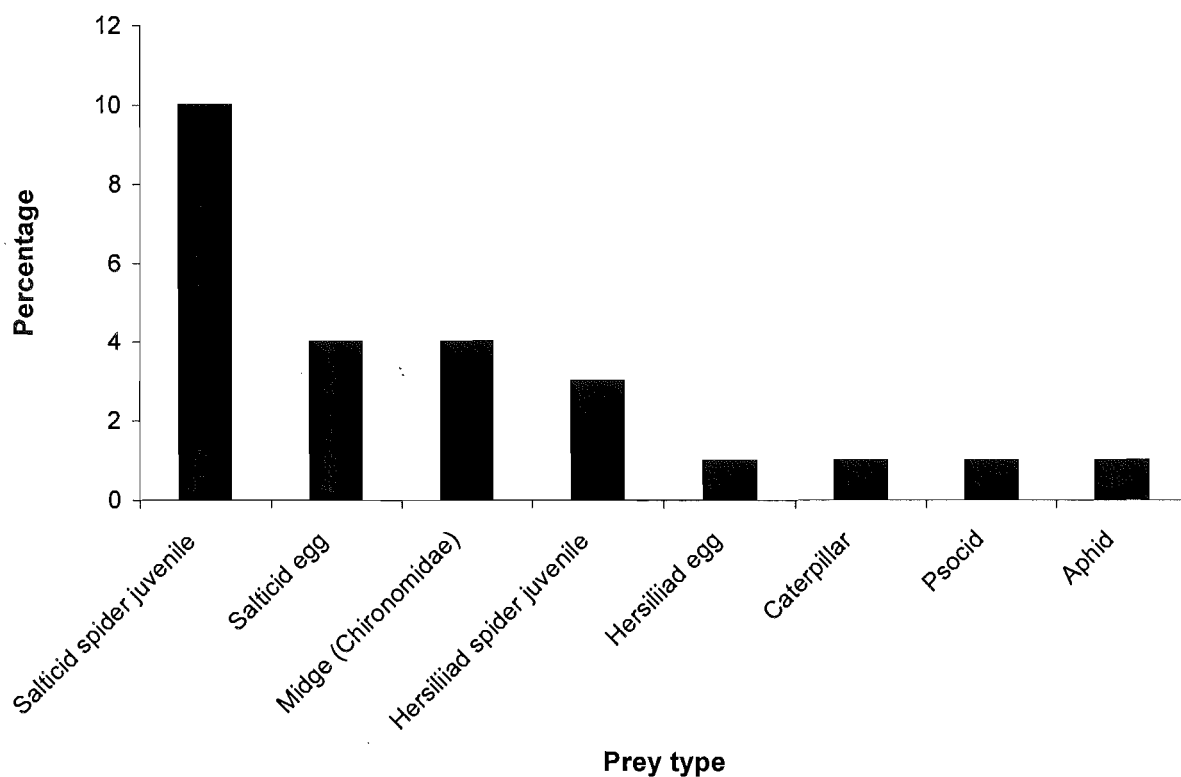


Fig 6.2. Summary of prey types from 71 observations in the field when *Myrmarachne melanotarsa* was found feeding

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Chapter 7

Prey-choice behaviour of *Myrmarachne melanotarsa*, a myrmecomorphic jumping spider from East Africa

Abstract

In a laboratory study using live prey and motionless lures, the prey preference of a social myrmecomorphic salticid, *Myrmarachne melanotarsa*, was investigated using simultaneous-presentation tests. In these tests, *M. melanotarsa* chose spiders as prey significantly more often than it chose insects, and it chose *Hersilia caudata* significantly more often than other spiders. How these preferences may affect the distribution of these spiders in the field is discussed.

INTRODUCTION

Conceptually, a predator's prey preference is distinct from its actual diet in nature (Morse 1980, Li and Jackson 1996). The term 'preference' refers to perceptual and decision-making processes, whereas 'diet' refers to what the predator actually eats. Although diet may be influenced by preference, it may also be influenced by active prey defence, prey availability, and other factors. Experiments designed to test perception and decision-making are the necessary basis for conclusions about a predator's preferences.

Jumping spiders (Salticidae) appear to be especially interesting subjects for prey-preference studies. They have unique, complex eyes, acute vision, and intricate vision-guided predatory strategies (Land 1974, Jackson and Blest 1982, Land 1985, Blest 1985). Experimental studies have shown that many salticid species can, by eyesight alone and in the absence of motion cues, distinguish between different kinds of prey at a distance of 10-40 body lengths (Harland *et al.*, 1999). There has been extensive research on the prey choice behaviour of two sizeable minorities in this large spider family, the araneophagic and the myrmecophagic species. Although most salticids may prey primarily on flies, moths, and other small soft-bodied insects (Richman and Jackson 1992), species from the genera *Brettus*, *Cocalus*, *Cyrbia*,

Phaeacius, and *Portia*, all in the subfamily Spartheinae, are araneophagic, having pronounced preferences for other spiders as prey (Jackson and Blest 1982; Jackson and Hallas 1986a, 1986b; Jackson 1990a, 1990b, 1990c). One particular population of one spartaeinae species, the Queensland *Portia fimbriata*, has a pronounced preference for other salticids as prey (Li and Jackson 1996). The myrmecophagic species are from the genera *Aelurillus*, *Chalcotropis*, *Chrysilla*, *Corythilia* (formerly *Stoidis*), *Habrocestum*, *Natta*, *Siler*, *Xenocytae* (formerly *Euophrys*) and *Zenodorus* (formerly *Pystira*). Most salticids appear to be adverse to attacking ants, but the myrmecophagic species actively select ants as preferred prey (Edwards *et al.* 1974, Cutler 1980, Jackson and van Olphen 1991, Jackson and van Olphen 1992, Li *et al.* 1996, Jackson *et al.* 1998, Li *et al.* 1999).

Species that resemble ants form another sizeable minority within the Salticidae, the myrmecomorphic species. The most thoroughly studied species are from the genus *Myrmarachne*, with this being the largest genus in the family Salticidae (Wanless 1978). There is now considerable evidence that the ant-like appearance of *Myrmarachne* and other myrmecomorphic salticids functions as Batesian mimicry (McIver and Stonedahl 1993, Cushing 1997). However, there have been no experimental studies of the prey-choice behaviour of myrmecomorphic salticids.

Here I investigate the prey preferences of a strikingly unusual salticid, *Myrmarachne melanotarsa*. This species is myrmecomorphic and also social (Weslowska and Salm 2002). An earlier study of this species from East Africa (Chapter 6) suggested the hypothesis investigated here: that besides being social and myrmecomorphic, *M. melanotarsa* is also araneophagic (i.e., that it is a salticid that prefers other spiders as prey). This hypothesis is tested here using live prey and stationary lures.

MATERIALS AND METHODS

In earlier studies (Li and Jackson 1996), three types of testing were used: alternate-day, simultaneous-presentation, and alternative-prey, with findings from the three being consistent. Here, only simultaneous-presentation testing was adopted, this being the testing method that requires the smallest sample sizes.

For live-prey tests, two prey individuals, each of a different type, were placed in a cylindrical cage (100 mm x 100 mm, height x diameter) with one *M. melanotarsa*. Observation ended when *M. melanotarsa* caught, and began feeding on, one of the two prey (i.e., it was not allowed to eat both), or when 30 min elapsed, whichever came first.

For lure-tests, the apparatus (Fig 7.1) was a clear glass box (100 mm x 35 mm: length x height). Each side of the box had a hole into which the open end of a clear vial (50 mm x 10 mm: length x diameter) was inserted. The lures were placed outside the vials and cage, but in view of the spider. To each side of the four vials, on opposite sides of the box, a lure made from one prey type was placed. Beside each of the other two vials, also on opposite sides of the box, were placed lures of a different prey type. One individual of *M. melanotarsa* was put in the apparatus and allowed 30 min to make a choice. *M. melanotarsa* could enter any of the four vials in the apparatus to get close to a lure. *M. melanotarsa*'s choice was recorded as the first vial that it entered and then remained in, for 60 s. The apparatus was cleaned with 80% ethanol followed by distilled water after each test and allowed to dry.

Prey used in the laboratory experiments were species that *M. melanotarsa* is known to encounter in the field (Table 7.1): juveniles of *Portia africana* and *Evarcha culicivora* (Salticidae); juveniles of *Nephilyngys* sp. (Tetragnathidae), a web-building spider near which the nest complexes of *M. melanotarsa* were often found; juveniles of *Hersilia caudata* (the nests of which were often the site for *M. melanotarsa* nest complexes); various insects which were commonly found in or near the salticid nest complexes (aphids (*Brevicoryne brassicae*;

Homoptera: Aphididae), lake flies (*Chaoborus sp.*; Diptera: Choboridae), moth flies (*Psychoda sp.*, Diptera: Psychodidae), and stemborers (*Chilo partellus*, Lepidoptera: Pyralidae)).

The prey spiders and insects were collected from the Thomas Odhiambo Campus (TOC) at Mbita Point, Kenya, from the same habitat as *M. melanotarsa*. Each lure was made by killing the spider or insect by asphyxiation using carbon dioxide, and then placing it in 80% ethanol for 1 h. The ethanol did not have any affect on the colour of the prey spiders and insects. The lure was then mounted on top of a disk-shaped piece of cork (see Li and Jackson 1996). Lures were kept in a refrigerator when not in use.

Laboratory cultures of *M. melanotarsa* were used, with standard laboratory procedures being adopted (see Jackson and Hallas 1986a). The laboratory photoperiod (L:D) was 12h:12h, with lights being switched on at 07h00, and all testing began between 08h00 and 11h00. Chi-square tests of independence were used when comparing results, with Bonferonni adjustments being made whenever data sets were compared more than once.

RESULTS

Data for the two salticid prey species (*P. africana* and *E. culicivora*) were pooled, as the results of prey preference tests for these two species were not significantly different in the live-prey tests ($N=62$, $\chi^2=2.25$, NS) or in the lure-tests ($N=33$, $\chi^2=1.08$, NS).

Data for the different insect prey species (lake fly, aphid, moth fly, and stemborer) were not significantly different from each other in live tests ($N=43$, $\chi^2=1.78$, NS) or in lure-tests ($N=33$, $\chi^2=1.71$, NS), and these data were pooled.

A ranking of prey preference was evident in live-prey tests (Fig 7.2 and Fig 7.3). *H. caudata* was chosen significantly more often than salticids ($\chi^2=63.00$, $p<0.001$), *Nephilyngys sp.* ($\chi^2=21.35$, $p<0.001$), or insects ($\chi^2=154.00$, $p<0.001$). Salticids were chosen significantly more often than *Nephilyngys sp.* ($\chi^2=32.4$, $p<0.001$) or insects ($\chi^2=80.25$, $p<0.001$).

Almost the same ranking was evident as in tests using lures instead of live prey (Fig 7.4 and Fig 7.5). Lures made from *H. caudata* were chosen more often than lures made from salticids (N=62, $\chi^2=60.70$, $p<0.001$), *Nephilyngys* sp. (N=34, $\chi^2=23.70$, $p<0.001$) or insects (N=81, $\chi^2=153.90$, $p<0.001$). Lures made from salticids were chosen more often than lures made from *Nephilyngys* sp. (N=66, $\chi^2=54.00$, $p<0.001$) or insects (N=177, $\chi^2=298.00$, $p<0.001$). However, there was no significant difference in how often *M. melanotarsa* chose *Nephilyngys* lures or insect lures (N=66, $\chi^2=0.92$, NS).

DISCUSSION

M. melanotarsa prey preference

In tests with live prey and in tests with lures, *M. melanotarsa* chose spiders more often than insects, and chose *H. caudata* more often than other spiders. Evidently, *M. melanotarsa* is a social myrmecomorphic salticid that is also araneophagic. More specifically, its preferred prey is hersiliids followed by salticids.

Myrmarachne melanotarsa is a small species, being as adults comparable in size to the early juvenile stages of common hersiliid and salticid species with which it is sympatric. In nature, *M. melanotarsa* may prey most often on the juveniles of hersiliids and salticids, and *M. melanotarsa*'s ant-like appearance may be especially significant when raiding salticid nests.

When ants invade the salticid nest complexes, the spiders tend to move quickly out of the ants' way (Chapter 2), suggesting that *M. melanotarsa*'s ant-like appearance may scare off the salticid adults, leaving *M. melanotarsa* free to eat the relatively defenceless juveniles. If this hypothesis is valid, *M. melanotarsa* may be an unusual example of how an ant-like appearance can function both as Batesian and as aggressive mimicry (McIver and Stonedahl 1993, Cushing 1997).

Myrmarachne melanotarsa and the nests of *H. caudata* were common on the same tree trunks in the field. *H. caudata* deposits its eggs within a discoid egg sac, covered with another

layer of dense silk. Once hatched, the hersiliid's spiderlings tend to stay within the eggsac for about a week before dispersing (Metwally *et al*, 2001). *M. melanotarsa* seems to be especially skillful at moving unnoticed into the eggsacs of *H. caudata*.

Insects, especially lake flies (Chaoboridae and Chironomidae) are exceedingly abundant in the field at Mbita Point, but *M. melanotarsa* seems to have specialized on specific concentrated food source generated by particular reproducing spiders. Interesting, as a social salticid, *M. melanotarsa* adopts these feeding sites for establishing its own colonies.

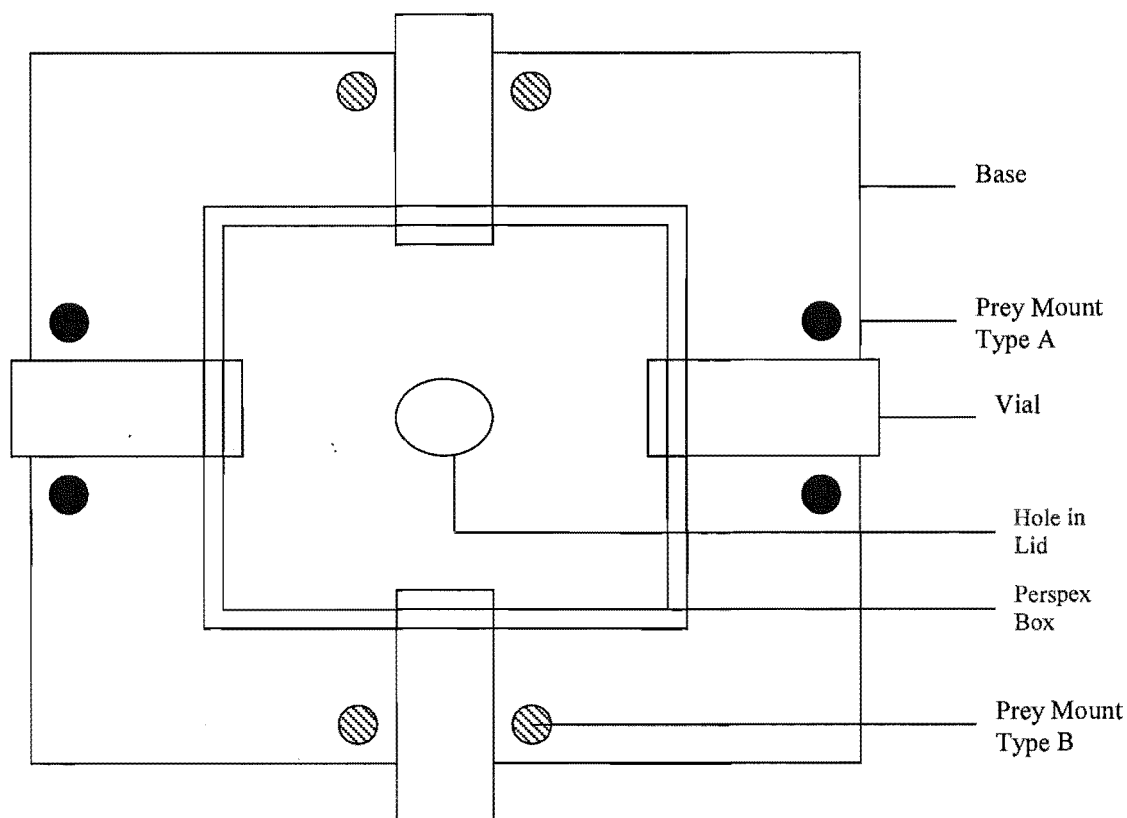


Figure 7.1. Prey-choice apparatus (not drawn to scale) made of clear glass. Square box (100 mm \times 100 mm, walls 35 mm high and 5 mm thick), with removable lid. Lid (100 mm \times 100 mm) held in place by 5-mm wide rim (5 mm from edge of box). Hole (diameter 16 mm) centred on each of four sides of the box (i.e. centre of hole 6 mm from top and 6 mm from bottom of box; equidistant from left and right sides of wall). Transparent glass vial (15 mm in diameter, 50 mm long) positioned in each of these four holes. Test spider enters vials from inside box. Test initiation: test spider enters through cork-plugged hole (diameter 16 mm) in lid and gains access to four vials (vials open on inside of box, but closed on outside of box). One mount on each side of each vial (pairs of prey mounts). Box sat on a 160 mm \times 160 mm plastic base, and each mount was placed on this base (secured with double-sided tape on the bottom of each cork). Each mount situated 10 mm to side of vial, and 15 mm from side of box.

Table 7.1. Arthropods used as prey (lures). Prey choice testing of *Myrmarachne melanotarsa*

Description	Species	Order and family	Body length of specimens used (mm)
Tree trunk spider	<i>Hersilia caudata</i>	Araneae, Hersiliidae	2.0
Jumping spider	<i>Evarcha culicivora</i>	Araneae, Salticidae	2.0
Jumping spider	<i>Portia africana</i>	Araneae, Salticidae	2.0
Web-building spider	<i>Nephilengys</i> sp.	Araneae, Tetragnathidae	2.0
Lake fly	<i>Chaoborus</i> sp.	Diptera, Chaoboridae	4.0
Moth fly	<i>Psychoda</i> sp.	Diptera, Psychodidae	2.0
Stemborer	<i>Chilo partellus</i>	Lepidoptera, Pyralidae	4.0
Aphid	<i>Brevicoryne brassicae</i>	Hemiptera, Aphidae	2.0

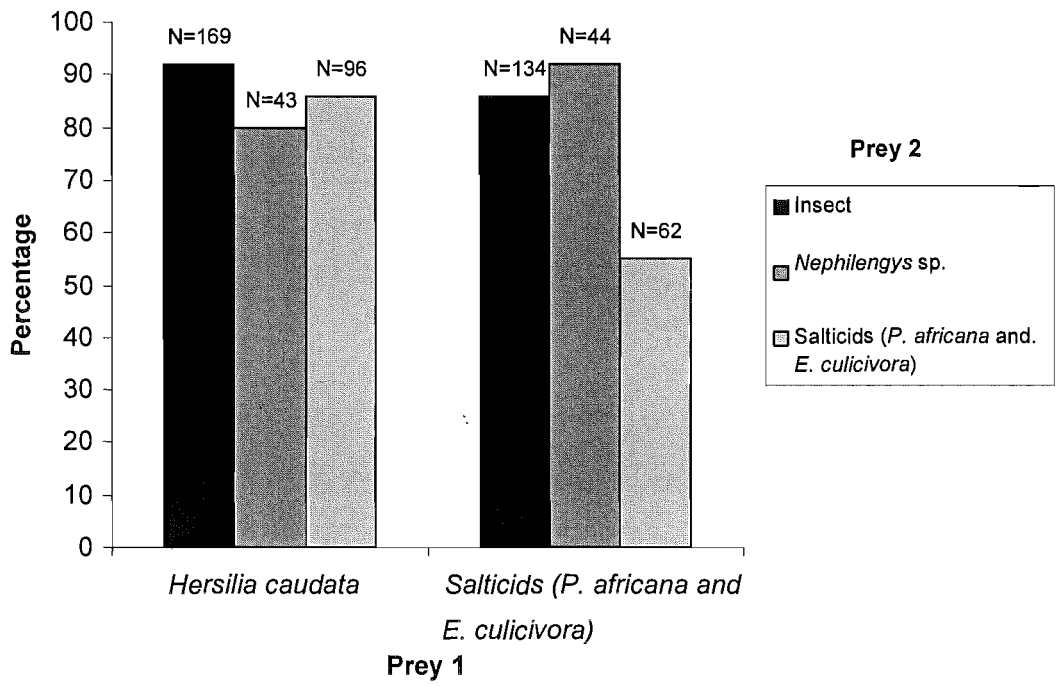


Fig 7.2. Preference of *Myrmarachne melanotarsa* for Prey 1 over Prey 2 in simultaneous presentation choice tests with live prey.

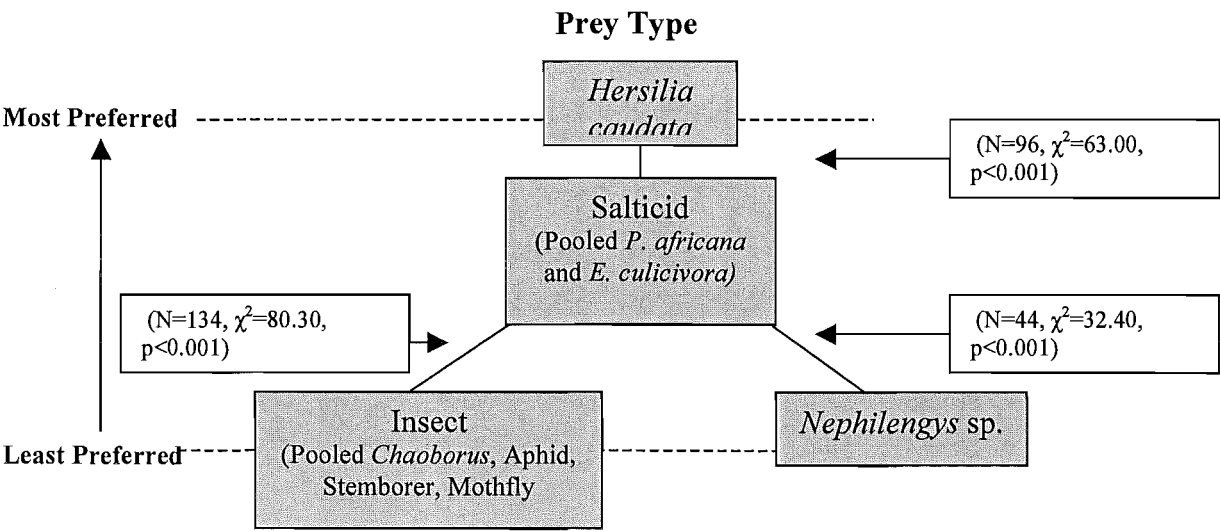


Fig 7.3. Prey preference rank of *Myrmarachne melanotarsa* for live prey species

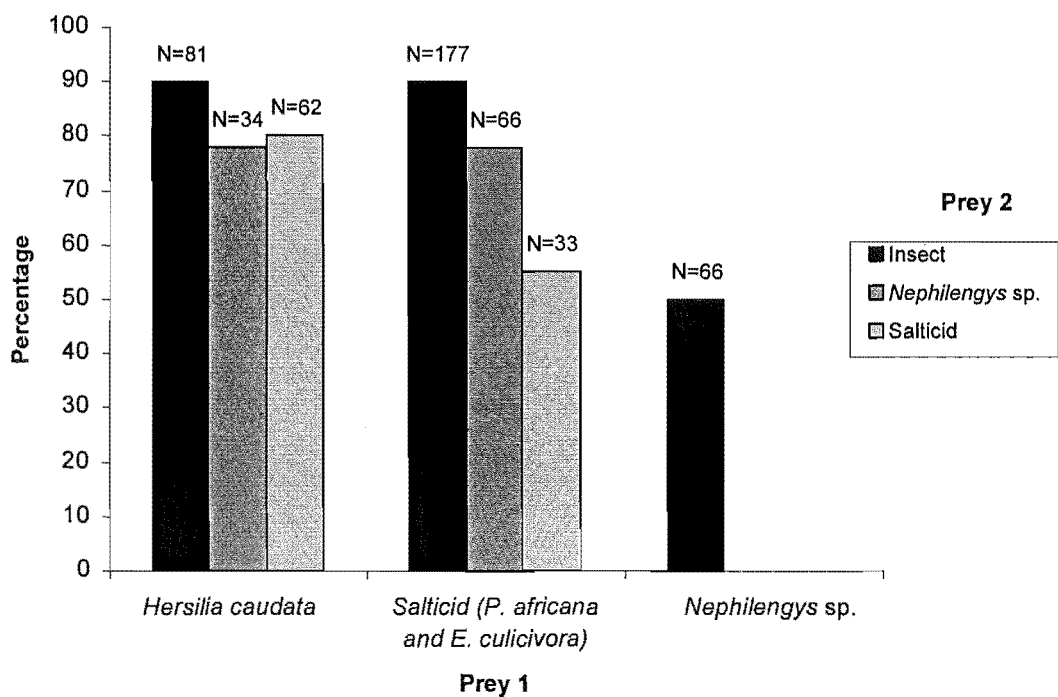


Fig 7.4. Preference of *Myrmarachne melanotarsa* for Prey 1 over Prey 2 in simultaneous presentation choice tests with lures.

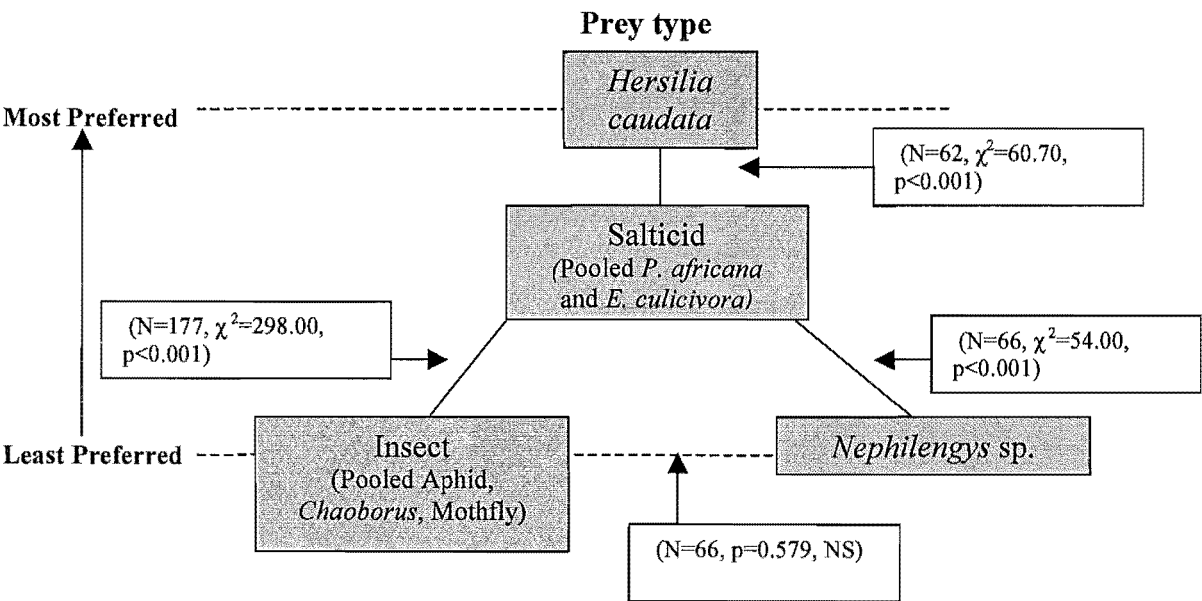


Fig 7.5. Prey preference rank of *Myrmarachne melanotarsa* for prey species lures

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Chapter 8

Influence of an ant, *Crematogaster* sp., on mouthing of silk by *Myrmarachne melanotarsa*, a myrmecomorphic salticid.

Abstract

Silk mouthing is a distinctive and frequent activity of *Myrmarachne melanotarsa*, a social salticid that mimics the ant *Crematogaster*. Here, the influence of prior presence of ants on colony silk is investigated in laboratory experiments. The findings suggest that ants leave secondary honeydew on the silk during their visits to the nest complexes and that *M. melanotarsa* and *Crematogaster* later feed on this by mouthing the silk.

INTRODUCTION

Mouthing silk is a dominant behaviour of *Myrmarachne melanotarsa* in the field (Chapter 6). Seeing this spider with its mouthparts pressed against the silk suggests that the spider is feeding on or drinking some substance from the silk. *Crematogaster*, the ant that *M. melanotarsa* mimics, frequently moves about on the nest complexes occupied by *M. melanotarsa*, suggesting that the ants active on the salticid nest complexes leave behind some substance that stimulates the mouthing of silk by *M. melanotarsa*. Here, I investigate this hypothesis.

MATERIALS AND METHODS

The basic procedure was to obtain nest complexes built by *M. melanotarsa* females, remove these females, allow ants (*Crematogaster*) to walk on the silk, and then test the reactions of other *M. melanotarsa* females to these nest complexes. The variable in the experiment was whether or not the nest complex had been visited by *Crematogaster* before testing began.

Each nest complex was obtained by putting 20 *M. melanotarsa* females in a cage at 09h00 and ensuring prey (chironomids) was continuously available for the following 10 days. At the end

of the 10-day period, preparation was successful if all 20 spiders were still alive and in a single nest complex. Preparation was unsuccessful if any spiders had died and if any spiders were in solo nests or if there were any nests other than the one nest complex in the cage. However, the spiders usually built a single nest complex during the 10-day period ('successful preparation'). At 0900 hours on day 10, all *M. melanotarsa* and all prey remains were removed from the cages in which nest-complex preparation had been successful, with the nest complex remaining intact in each cage.

Each cage, with an unoccupied nest complex inside, was assigned at random to one of two groups. Group A: 10 ant workers (*Crematogaster*) were placed in the cage immediately after removing the spiders and prey remains. Group B (control): no ants were put into the cage.

The ants were removed 24 h after being put into the cage (0900 hours on day 11). Five *M. melanotarsa* females were placed in each cage immediately the ants were removed and observed for the following 60 min. The outcome of a test was recorded as a 'response' whenever at least one of the five spiders mouthed the silk.

RESULTS

Responses by *M. melanotarsa* were significantly more common in Group A (cages that had been occupied by ants) than in Group B (control) (Fig 8.1, test of independence, $\chi^2=10.266$, $p<0.01$).

DISCUSSION

Honeydew, the sugary excreta of coccids and other homopterans (Buckley 1987, Gullan 1997), is frequently a food source used by ants (Völkl *et al.* 1999). Reports of spiders feeding on honeydew are scarce, but *M. melanotarsa*, a salticid that mimics the ant *Crematogaster*, has been observed feeding on honeydew in the field. *Crematogaster* feeds on honeydew (Sudd & Franks

1987) and it has been suggested that *M. melanotarsa* finds honeydew sources by following the marching columns of *Crematogaster* (Chapter 5). The findings reported in this chapter suggest that *Crematogaster* may also bring honeydew to *M. melanotarsa*.

The findings in this chapter imply that *Crematogaster* leaves a stimulus on nest silk to which *M. melanotarsa* responds by mouthing. Perhaps what is left behind is sugar on which *M. melanotarsa* feeds. Perhaps much of the sugar in honeydew is not removed during a single passage through the ant's digestive tract. This sugar may become 'secondary honeydew' when deposited as excreta by the *Crematogaster* individuals walking on the silk.

Workers of *Crematogaster* have also been seen with their mouthparts pressed into the silk, suggesting that they also feed or drink from the silk. Perhaps they too feed on the sugar from ant excreta. However, another hypothesis might be considered. Ants sometimes protect other insects, as well as plants, and various insect (Axén and Pierce, 1998; Völkl *et al.*, 1999) and plant species (Keeler, 1980; Barton, 1986) are known to encourage the company of ants by depositing chemical lures. The company of *Crematogaster* may also function to protect *M. melanotarsa* against the attacks of predators (see Chapter 8). For future work, consideration should be given to the possibility that, when mouthing silk, *M. melanotarsa* is depositing substances that attract *Crematogaster*. However, this hypothesis is less convincing than the first hypothesis because mouthing silk increased after, not before, the ants had been present.

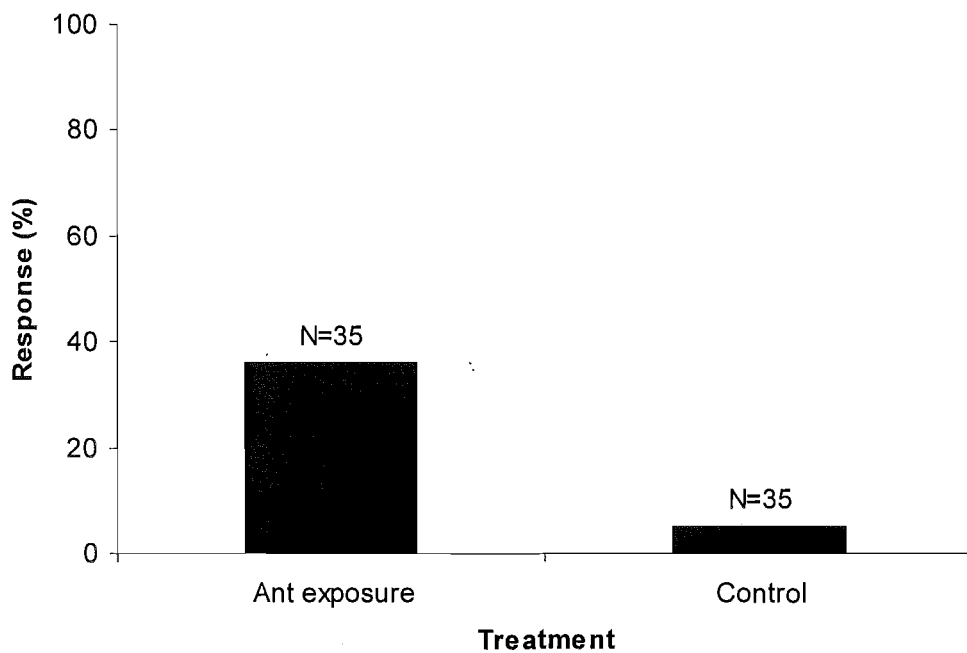


Fig 8.1. Comparison of percentage of tests in which there was a response. Ant Exposure: *Crematogaster* sp. had access to nest silk before testing (N=35 tests). Control: silk not contacted by *Crematogaster* sp. (N=35 tests) before testing. Response (at least one *Myrmarachne melanotarsa* female mouthed silk).

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Chapter 9

Collective defence by *Myrmarachne melanotarsa*, a social ant-like jumping spider

Abstract

Myrmarachne melanotarsa, a salticid spider, resembles the ant *Crematogaster* sp. *Crematogaster* sp. and *M. melanotarsa* both live in groups, and often they are found in mixed-species groups. An experimental study, using two large salticid species (*Hyllus* sp. and *Plexippus* sp.) as the predators, provides evidence that predators that are averse to attacking *Crematogaster* sp. are also averse to attacking *M. melanotarsa* and that these predators are even more averse to attacking a member of a group, where the group consists of *Crematogaster* sp. only, *M. melanotarsa* only or *M. melanotarsa* with *Crematogaster* sp. Evidently, grouped individuals of *M. melanotarsa* are collectively Batesian mimics of grouped individuals of this salticid's social model, *Crematogaster* sp.

INTRODUCTION

In a Batesian-mimicry system, palatable prey individuals deceive potential predators by resembling unpalatable models (Wickler 1973). Here we investigate a Batesian mimicry system in which the models are ants (Formicidae), the mimics and the predators are jumping spiders (Salticidae), and the mimics are also social. My hypothesis is that, for social ant mimics, Batesian mimicry is more effective when 'in a crowd' rather than alone, where 'in a crowd' means in the company of the model (ants), or other ant mimics (conspecific individuals) or both (mixed groups consisting of the model and conspecific individuals).

Salticids are unique spiders because of their complex eyes, acute vision and intricate vision-guided predatory strategies (Land 1969, Jackson and Pollard 1996, Harland and Jackson 2000). A sizeable minority of the Salticidae are ant-like in appearance (myrmecomorphic) (Reiskind 1977, Wanless 1978, Edmunds 1978, Parker and Cloudsley-Thompson 1986, Jackson and Willey 1994). Ants are the most abundant insects in most terrestrial habitats (Holldobler and Wilson 1990), but their defences (e.g., powerful mandibles, poison-injecting stings, formic

acid and communal defences (Eisner 1970, Blum 1981) appear to present formidable challenges to many predators that routinely take other arthropods in the same size range. As a result, some of these predators, including many salticids, avoid coming into close proximity to ants (Bishop and Bristowe 2001; Nelson *et al.* 2004). Predators that avoid ants, including ordinary (i.e., non-ant-like) salticids, also avoid ant-like salticids (Cutler 1991, Nelson *et al.* 2004.). Apparently, myrmecomorphy functions as Batesian mimicry.

Here I investigate something different. Although usually not stated explicitly in this way, the consensus view is probably that, for myrmecomorphic salticids, Batesian mimicry is based on each single salticid resembling a single ant. However, ants are distinctive not only as individuals but also because they are social. Sociality may often be an important factor in making ants unattractive to potential predators, the most obvious reason being that a group of ants may mount a communal defence. A few spiders, including a few salticid species, are social, but social spiders generally are not ant mimics. *Myrmarachne melanotarsa* is an exception. This East African myrmecomorphic salticid is also social (Wesolowska and Salm 2002). The model of *M. melanotarsa* is *Crematogaster* sp., a myrmicine ant. *M. melanotarsa* and *Crematogaster* sp. are small arthropods (adult body lengths c. 3mm), normally found in groups, and these two species are routinely found in the same groups. Potential predators that are reluctant to attack an isolated ant may be even more reluctant to attack an ant found grouped with other ants. The same reasoning can be applied to the mimic. My hypothesis ('collective mimicry') is that predators reluctant to attack an isolated ant-mimic individual are even more reluctant to attack an ant-mimic individual found as a member of a group of ants or other ant mimics or both.

In laboratory experiments, I test this prediction using as predators another two salticid species, *Hyllus* sp and *Plexippus* sp. These two salticid species are sympatric with and considerably larger than *M. melanotarsa* and *Crematogaster*. Although the typical prey of *Hyllus* sp. and *Plexippus* sp. are insects other than ants, preliminary laboratory testing

confirmed that both of these species will occasionally attack small myrmecomorphic salticids and ants, including *M. melanotarsa* and *Crematogaster*, and they readily prey on small non-myrmecomorphic salticids.

MATERIALS AND METHODS

The study site was on the shore of Lake Victoria in western Kenya at Mbita Point (the Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology). All salticids were from laboratory cultures begun from specimens collected at Mbita Point. Basic rearing and testing procedures were as in earlier salticid studies (see Jackson and Hallas 1986). Insects were collected in the field (Mbita Point) as needed. In experiments, the predator (*Hyllus* sp. or *Plexippus* sp.) was always a juvenile (body length 8 mm), and the prey were adult females of *M. melanotarsa*, *Crematogaster* workers, juveniles of *Menemerus* sp. A (a social salticid species that does not resemble ants), and adults of *Chaoborus* sp. (Chaoboridae) ('lake flies'). All prey were 3 mm in body length. Hunger level was standardised by keeping all individuals of *Hyllus* sp. and *Plexippus* sp. without prey for 15 days immediately before testing. All individuals of *M. melanotarsa* were fed to satiation before testing. The laboratory-reared predators had no prior contact with the prey species used for testing and the laboratory-reared *M. melanotarsa* had no prior contact with the predators.

The testing apparatus was a square plastic cage (100 x 100 x 35 mm) with one cork hole for introducing prey centred on each side and a hole for introducing the predator centred on the bottom of the cage. The cage rested on a platform that provided ample space for reaching the hole in the bottom of the cage. All holes were 10 mm in diameter, and all were kept plugged with a cork except when introducing prey or predators.

M. melanotarsa and *Menemerus* sp. A were put in test cages 10 days before the testing began and fed every second day to satiation. All prey, prey remains, nests and draglines were removed from the cage containing the salticids at 08h30 on the morning of testing. Testing

began at 09h00 (laboratory photoperiod, 12 L: 12 D; lights on at 08h00). Ants and lake flies were put in the cages 15 min before testing began.

Each predator was taken into a plastic tube (diameter 10 mm; length 20 mm) at 08h30. Each end of the tube was plugged with a cork. Testing began by removing the cork from the hole in the bottom of the cage and from one end of the tube and then connecting the open end of the tube to the open hole in the cage. The predator usually walked into the cage within 10 min of connecting the tube. Otherwise, it was gently coaxed out of the tube and into the cage by removing the cork from the other end of the tube and inserting a small soft brush. Testing lasted 60 min. The predator and potential prey were observed for the entire 60-min test period. No individual predator or prey was used in more than one test. There were 10 groups of tests (50 replicates per group) for each predator, each group defined by the type (s) and numbers of prey in the cage. Chi-square tests of independence were used when comparing groups, with Bonferonni adjustments whenever data sets were compared more than once.

RESULTS

As there were no significant differences (in all instances, $P > 0.1$) between the *Hyllus* and *Plexippus* for any of the experiments, data for the two species are pooled below and referred to jointly as 'predators'. When data are considered from testing predators with groups of 10 prey individuals, the expression 'made a kill' is used for instances in which the predator killed one or more of the 10 prey individuals.

In all instances, the potential prey attacked by the predator died. Most potential prey that were killed were also fed on for at least 15 min (i.e., the predator held on to, and masticated, the captured arthropod). The only exceptions were the solitary ants. All were released soon after being killed (1 after 10 min; 2 after 6 min; 2 after 2 min; 3 after less than 1 min).

The number of predators that killed solitary ants (8% killed) was not significantly different from the number that killed solitary *Myrmarachne* (15% killed) (Fig 9.1, NS, $p = 0.12$).

These data were pooled (12.5% of 200) and referred as 'solitary *Myrmarachne*-ant'. The data for number of predators that killed solitary lake flies (97%) and the number that killed solitary *Menemerus* (79%) were pooled (88% of 200) and referred as 'solitary *Menemerus*-fly'.

The number of predators that made kill on *Crematogaster* in a group of ten (0 of 100) was not significantly different from the number that made a kill on *M. melanotarsa* (1 of 100) in a group of ten (Fig. 9.1, NS, $p=0.3167$). These data were pooled (0.5% of 200) and referred as 'grouped *Myrmarachne*-ant'. The number of predators that made a kill on lake flies in groups of 10 (%) was not significantly different from the number that made a kill on *Menemerus* in groups of 10 (%) (Fig. 9.1, NS, $p=0.08$). These data were pooled (% of 200) and referred as 'grouped *Menemerus*-fly'.

Compared with how many predators killed solitary *Myrmarachne*-ants (11.5%), significantly more predators killed solitary *Menemerus*-flies (88.0%) (Table 9.1, $\chi^2=234.10$, $P<0.001$). Compared with how many predators made a kill on grouped *Myrmarachne*-ants (0.5%), significantly more predators made a kill on grouped *Menemerus*-flies (90.5%) (Table 9.1, $\chi^2=326.65$, $P<0.001$).

When tested with grouped prey, predators sometimes killed as many as four lake flies or *Menemerus*, but there were no instances in which a predator killed more than one ant or more than one *Myrmarachne*. There were no tests in which the predator killed even one of the ten ants in a group, and there was only one test in which a predator (*Hyllus*) killed one of the ten *Myrmarachne* individuals in a group. Nor were there any tests in which predators killed even one prey individual (ant or *Myrmarachne*) in a mixed group of ten. All of these data were pooled (0.2% of 500) and referred to as 'all grouped *Myrmarachne*-ants'. Compared with how many predators killed solitary *Myrmarachne*-ants, significantly fewer made a kill on 'all grouped *Myrmarachne*-ants' ($\chi^2= 32.75$, $P<0.001$). However, the number of tests in which the predators killed solitary *Menemerus*-flies was not significantly different from the number of

tests in which predators made a kill on grouped *Menemerus*-flies (Table 9.1, $\chi^2 = 0.65$, $P = 0.4195$).

DISCUSSION

Solitary *Chaoborus* (lake flies) and solitary *Menemerus* both appear to be, for *Hyllus* and *Plexippus*, palatable prey (i.e., these were arthropods that these particular predators readily killed and ate). The rare instances in which the predators killed *Crematogaster* (ants) or *M. melanotarsa* (myrmecomorphic salticids) suggest that the ant mimic (*M. melanotarsa*), but not the ant, is palatable (i.e., the predator always spent considerable time feeding on the ant mimic it killed, but never held on to killed ants for more than 10 min. For *Hyllus* and *Plexippus*, a solitary *M. melanotarsa* is apparently a Batesian mimic of a solitary ant.

In 60-min tests, many individuals of the lake flies and many individuals of *Menemerus* survived (i.e., the predator never killed more than 4 of the 10 individuals in a group), and it might be tempting to interpret these findings as evidence of a selfish-herd effect (see Hamilton 1971). However, our data are not adequate for evaluating this hypothesis, nor was evaluating this hypothesis one of our goals. In particular, we do not know what would happen during longer test intervals with more space available for the prey. Our interest was, instead, to compare how often the predator attacked and killed solitary prey with how often it attacked and killed any prey at all in a group. We found no evidence that the predators perceived a group of lake flies or of ordinary salticids as aversive (i.e., there was no significant difference in how often the predator attacked the solitary prey and how often it attacked at least one prey in a group).

Fewer of the predators made attacks at all during encounters with *Crematogaster* or *M. melanotarsa* in groups than in encounters with solitary *Crematogaster* or *M. melanotarsa*. Groups of these two species were evidently perceived by the predators as more aversive than solitary individuals of the same species. For *Hyllus* and *Plexippus*, a group of *M. melanotarsa*

appears to be Batesian mimic of a group of *Crematogaster*. With group size constant (always 10), there is also no evidence that the predator distinguishes between pure groups (i.e., groups of only ants or of only ant mimics) and mixed groups (i.e., groups containing both species).

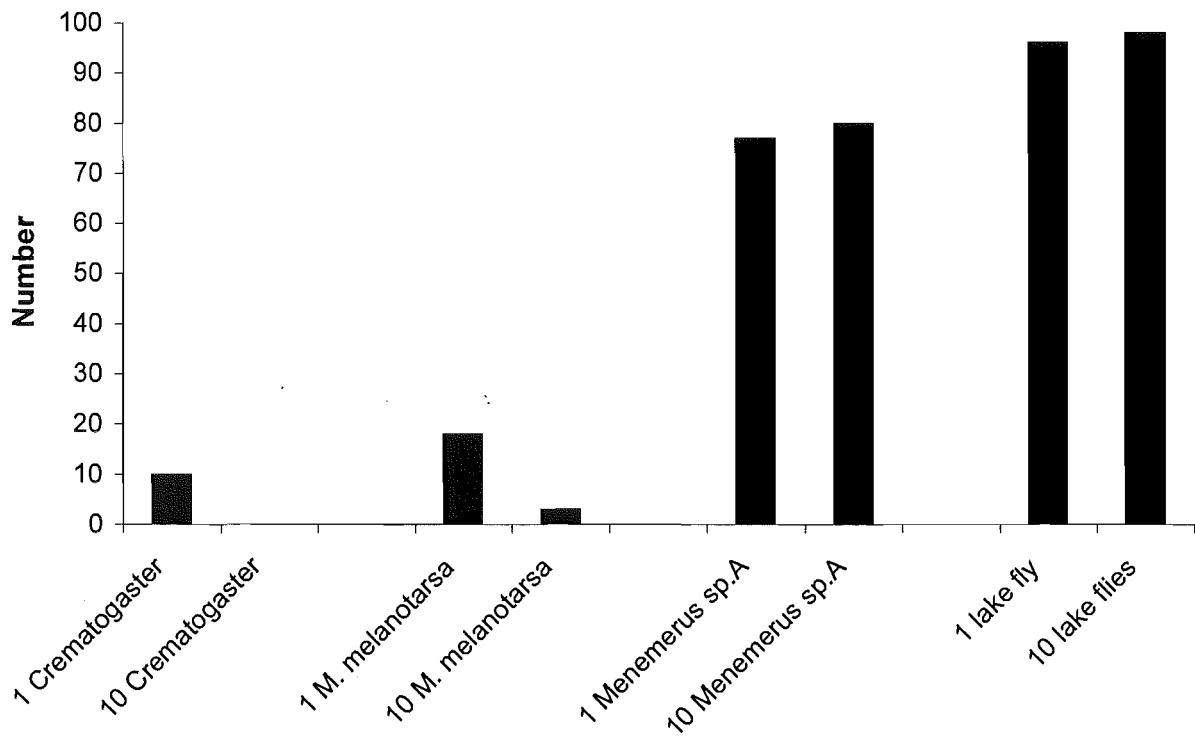


Figure 9.1. Percentage of tests during which predators (pooled data from using two large salticid spider species, *Hyllus* sp. and *Plexippus* sp.) killed at least one prey from eight different prey categories. For each prey category, N=100.

Table 9.1. Summary of test outcomes. Pooled data from testing with two predator species (*Hyllus* sp. and *Plexippus* sp.) and from pooling for different categories of prey (Group).

Group	Number of tests during which there was predation
One <i>Crematogaster</i> sp. & one <i>Myrmarachne melanotarsa</i>	23 of 200
One lake fly & one <i>Menemerus</i> sp.A	176 of 200
Ten <i>Crematogaster</i> & ten <i>Myrmarachne melanotarsa</i> *	1 of 200
Ten <i>Menemerus</i> sp.A & ten lake flies *	181 of 200
Mixed groups <i>Crematogaster</i> & <i>Myrmarachne melanotarsa</i> *	0 of 300
All grouped	1 of 500
*One or more of the 10 prey killed	

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Chapter 10

Stealing from ants, a feeding tactic adopted by an East African jumping spider.

Abstract

Instances of *Menemerus* sp. A, a salticid spider, stealing prey from *Crematogaster*, an ant, are documented from observation in East Africa. *Menemerus* sp. A takes up position beside ant columns and observes the passing ants carrying their collected food. When an ant approaches the spider carrying a suitable prey item, *Menemerus* sp. A intercepts the ant and pulls the prey away from the ant.

INTRODUCTION

In the tropics, ants (Formicidae) are the dominant insects (Hölldobler & Wilson 1990) and jumping spiders (Salticidae) are the dominant spiders (Coddington & Levi 1991), but we are only beginning to understand how salticids and ants interact. Salticids are unique among spiders because of their complex eyes (Land 1969, Blest *et al.* 1990), exceptionally acute vision (Land & Nilsson 2002) and intricate vision-guided predatory behaviour (Jackson & Pollard 1996). Most species in this large family of about 5,000 described species (Platnick 2002) appear to be active hunters that prey primarily on a variety of insects, but typically not on ants. Ants may be important predators for many salticids (Nelson *et al.* 2004), and many salticid species may detect ants by sight and then avoid coming close. However, there is also a large minority of salticids (the ‘myrmecophagic species’) that selects ants as preferred prey (Li & Jackson 1996).

Another large minority, the ‘myrmecomorphic species’ resemble, but typically do not eat, ants (Edmunds 1978, Wanless 1978). The ant-like appearance of these salticids apparently functions as Batesian mimicry (Edmunds 1978, Cutler 1991), with predators that are averse to attacking ants also being averse to attacking the myrmecomorphic salticid (Nelson *et al.* 2004, Chapter 9).

Robbing ants is yet another feeding strategy adopted by a few salticids, the best known example being *Cosmophasis bitaeniata*, an Australian salticid that preys on the larvae of weaver

ants, *Oecophylla smaragdina* (Allan and Elgar 2001). This salticid does not prey on adult ants and it is not particularly ant-like in appearance. However, *C. bitaeniata* is a chemical ant mimic. By mimicking the cuticular hydrocarbons of *O. smaragdina* (Allan and Elgar 2001), it can enter the weaver ant's nest where it feeds un-molested on the ant's larvae.

However, there is an earlier report of a salticid adopting a different style of stealing from ants. Bhattacharya (1936) summarized, and documented with photographs, observations of the juveniles of a salticid in India, *Menemerus bivittatus* (formerly '*Marpissa melanognathus*'), snatching food out of the mandibles of fire ants, *Solenopsis geminate*. Bhattacharya suggested that the primary foraging strategy of the juveniles of this salticid is removing eggs and other food directly from the mandibles of ants.

Here we document prey-stealing behaviour by another salticid species, a currently undescribed species of *Menemerus* (referred to as '*Menemerus* sp. A') from East Africa. As with Bhattacharya's earlier study, this is not a comprehensive quantitative study. This is instead a preliminary qualitative report based on casual observations made during the course of other research in the same study site.

MATERIALS AND METHODS

The genus *Menemerus* is clearly distinct from other salticid genera, but it can be difficult to distinguish between the species within the genus (Wesolowska 1999). *Menemerus* sp. A, the species in our study, is currently undescribed. The study site was Mbita Point (the Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology). Mbita Point is on the shore of Lake Victoria in western Kenya. In this habitat, midges (Diptera: Chironomidae & Chaoboridae), known locally as 'lake flies', are exceedingly abundant (Beadle 1981), often coming off the lake in swarms that cover the walls of buildings. Having short life spans, the lake flies soon create enormous piles of corpses, which soon attract scavenging ants.

Our goal being to document qualitatively *Menemerus* sp. A's foraging tactic (stealing from ants), observations were conducted opportunistically when *Menemerus* sp. A was seen in the vicinity of ants. Individuals that oriented toward ants were watched (or sometimes video taped) until they stole prey or turned away, or until 30-60 min elapsed if they remained quiescent.

RESULTS

The sequences observed always took place on walls of buildings, and in all instances the ant workers belonged to the genus *Crematogaster* (body length c 3 mm). Groups of *Menemerus* sp. A normally live in nest complexes (Jackson 1986), and these nest complexes are especially often on the walls of the same buildings frequented by scavenging ants. All observed stealing sequences took place either in the morning (before 1100 hours) or in the late afternoon (after 1700 hours). The individuals of *Menemerus* sp. A were adult females (body length c 6 mm), adult males (body length c 6 mm) and nearly mature juveniles (body length 4-6 mm). *Crematogaster* tended to be moving actively in columns along walls at these same times of the day, with many individuals carrying lake fly corpses.

Stealing was typically structured around in four stages (Fig 10.1). First *Menemerus* sp. A 'oriented' toward an ant that had a lake fly in its mandibles (i.e. it turned so that its anterior-median eyes faced directly toward the ant, and it continued to turn so as to maintain this orientation to the moving ant). Most sequences ended at this stage (i.e., the ant moved out of range and *Menemerus* sp. A did not approach). Occasionally *Menemerus* sp. A proceeded to the next stage, 'interception' (i.e., it moved in front of an ant, effectively blocking the ant's path and halting the ant's progress). When intercepting, *Menemerus* sp. A usually took a veering path and approached the ant column at an angle, typically with the salticid moving in on a path 20-45° off from straight ahead of the targeted ant's forward path. When *Menemerus* sp. A stepped in front

of the ant, the ant usually slowed down and veered to the side, or else the ant stopped momentarily.

With the ant moving slowly, if not standing still, *Menemerus* sp. A usually went to the next stage, 'snatching' (i.e., it suddenly extended its rear legs, moving its body 1-2 mm forward and brought its chelicerae into contact with the lake fly in the ant's mandibles, took hold of the lake fly and then immediately and rapidly stepped backwards a few millimetres, pulling the lake fly away from the ant). *Menemerus* sp. A next went hastily to the fourth stage, 'retreating' (i.e., it turned and walked rapidly away, holding on to the lake fly). Once about 100 mm away from the ant column, *Menemerus* sp. A stopped and ate the lake fly.

Feeding typically lasted 1-10 min, after which *Menemerus* sp. A dropped the lake fly and walked away. Often it returned to the ant column and stole another lake fly from the ants, and as many as four lake flies were sometimes stolen in succession.

I made about 30 observations in the field of *Menemerus* sp. A stealing lake flies from *Crematogaster*. In each instance, the lake fly appeared to be already dead when the salticid snatched it. Body lengths of the lake flies appeared to be between 5 and 10 mm. No attempt was made to measure or identify (to species or genus) the highly masticated lake flies. I also observed a few instances of *Menemerus* sp. A pulling other objects from *Crematogaster*'s mandibles (an ant egg, X1; an apparently dead mayfly, X1; what appeared to be plant material, X3; a dead *Crematogaster* worker, X3). All of these objects were comparable to lake flies in size. *Menemerus* sp. A subsequently ate the mayfly and the ant egg, but released and moved away from the plant material and the dead ant a few seconds after contact. There were also five instances in which *Menemerus* sp. A released and moved away from a dead lake fly snatched from an ant within a few seconds after contact.

There were at least 20 instances in which I observed *Menemerus* sp. A orienting briefly toward an ant that had empty mandibles, but it never approached these ants. There were also at least 20 instances in which *Menemerus* sp. A oriented briefly toward ants that were carrying

objects other than lake flies and then failed to approach. There were seven instances of seeing *Menemerus* sp. A not only orient toward an ant that was carrying an object other than a lake fly (five carrying plant material and two carrying a dead conspecific ant worker) but also intercept the ant and then moved away without snatching the object in the ant's mandibles.

DISCUSSION

Evidently stealing from ants is a prey-capture tactic of at least two salticid species, *Menemerus bivittatus* in India (Bhattacharya 1936) and *Menemerus* sp. in East Africa. Although Bhattacharya provided less descriptive detail, it seems that the stealing sequences of the two species are similar in basic respects: the salticid orients toward an ant that is carrying potential food, intercepts it, snatches the food away and then retreats to feed.

Bhattacharya (1936) did not indicate how many times he observed stealing and he referred to what the spiders stole as simply 'food and eggs'. He did not indicate the size of the spiders, the food and the ants, but he indicated that all of his observations were of juvenile spiders doing the stealing. He observed *M. bivittatus* adults stalking, capturing and feeding on house flies, *Musca domestica*, and he suggested that stealing from ants may be the primary foraging tactic of *M. bivittatus* juveniles. Perhaps this conclusion is correct for *M. bivittatus*, but it appears to be inapplicable to the East African *Menemerus* sp. A.

We observed adults of both sexes and the larger juvenile stages of the East African *Menemerus* sp. A stealing from *Crematogaster* workers. Adults of *Menemerus* sp. A and *Crematogaster* are comparable in size and perhaps the early instars of the spider are too small to take on an ant. However, neither the juveniles nor the adults *Menemerus* sp. A appear to forage primarily by stealing from ants. This a very abundant salticid at Mbita Point, and we have witnessed hundreds of instances of adult males, adult females and juveniles stalking, capturing and feeding on living lake flies that they encountered free on the walls of buildings rather than in the mandibles of ants.

It is not clear why the East African *Menemerus* sp. A sometimes adopts this alternative foraging tactic, stealing from ants. It would be hard to argue that the spider needs the ant to find lake flies. Appropriate targets for the typical salticid mode of prey capture, stalking and leaping on living prey, seem always to be available in large numbers on the walls of buildings. It would also be hard to argue that the spider needs the ant to overpower these soft-bodied insects that have no apparent ability to injure a hungry salticid.

Seeing the walls of buildings covered by these insects, it is tempting to envisage a salticid grazing on them as though they were antelopes grazing on grass. This is a misleading image. Capturing a living lake fly is not effortless for the salticid. For starters, the lake fly can defend itself by flying away. Success depends on slowly stalking until close enough to gauge an accurate leap. Stalking sequences typically take many minutes, compared with a few seconds to intercept an ant.

Decision making is another potential problem for the salticid. When we casually glance at a wall of a building, we may get a misleading impression because it is not immediately obvious that many of the lake flies on the wall are already be dead. Dead lake flies may remain in lifelike posture on the wall. The presence of so many spiders at the Mbita Point appears to be one of the reasons for this. Stray silk lines hold the dead lake flies in place. *Menemerus* sp. A and other salticids are often seen stalking these dead flies, leaping on them and then releasing them almost immediately. There were, however, only five instances in which we observed *Menemerus* sp. A immediately release and move away from a dead lake fly it had snatched from an ant. Perhaps one of the primary advantages of stealing from ants is that the salticid can rely on the ant to select the lake flies that are still palatable.

It is interesting that Bhattacharya's (1936) observations were also on a species of *Menemerus*, and it would be interesting to determine whether this foraging method is especially common in this particular genus. However, despite a wide variety of salticids being abundant at Mbita Point, including at least three species of *Menemerus*, it was only *Menemerus* sp. A. that

was observed stealing from ants. *Menemerus* sp. A appears to be the most abundant species of *Menemerus* at Mbita Point, and this might be part of the explanation for why only this species was observed stealing from ants. Another factor may be the relative sizes of the ants, the food carried by the ants and the salticids.

Menemerus bivittatus adults are considerably larger than *Menemerus* sp. A adults, and it is interesting that all of the individuals of *M. bivittatus* that Bhattacharya (1936) observed stealing from ants were all juveniles. Although it is not possible to ascertain the size of the juveniles he observed, the ants in his observations, *Solenopsis* (body length c. 6 mm), were larger than the ants in my observations, *Crematogaster* sp. (c. 3 mm). In my observations, salticid, ants and the parcels stolen from the ants (lake flies) were all comparable in size. Perhaps, on the whole, the trend is for *Menemerus* individuals, whatever the species, to steal from ants when the ants and the parcels to be stolen are close to their own size. In our study site, a small ant, *Crematogaster*, was the dominant scavenger. It would be interesting to make more observations in habitats where other ant species are dominant.

Fig 10.1. Sequence in which *Menemerus sp.A* steals lake fly from ant (*Crematogaster*) in a column moving along wall of building at Mbita Point



10.1.a. Watching ant column



10.1.b. Approaching an ant that is carrying lake fly



10.1.c. Intercepting ant in column



10.1.c. Moving away with lake fly

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Chapter 11

The natural history of salticid-eating assassin bugs

Abstract

Baseline information is provided on the predatory behaviour of *Scipinnia repax* and *Nagusta* sp., two East African reduviid species that prey on social salticids. Salticids appear to be the preferred prey for both these reduviids, and *S. repax* also appears to prefer *Nagusta* sp. as prey. Questions raised by this information are considered in later chapters.

INTRODUCTION

With more than 2000 species, Reduviidae is one of the largest families of heteropteran insects (Miller 1956). On the whole, reduviids appear to be active insect-eating predators (Schuh and Slater 1995), with a few species specialising at preying on particular types of insects. However, few details are available about the predatory behaviour of most the species in this large family. This chapter is an initial report on the natural history of *Scipinnia repax* and *Nagusta* sp., East African reduviids that are routinely found standing on the silk of salticid nest complexes in the Lake Victoria region of East Africa (Chapter 2). This summary of these two species' natural histories raises questions that will be investigated more thoroughly in later chapters.

MATERIALS AND METHODS

Observations were made opportunistically in the field whenever these reduviids were seen on or in the vicinity of salticid nest complexes at Mbita Point (Thomas Odhiambo Campus of the International Centre for Insect Physiology and Ecology) in western Kenya. Individual observation periods lasted 5-60 min. Prey capture was also observed using captive specimens in the laboratory.

OBSERVATIONS

Location of the reduviids in the Field

Almost all of the individuals of *S. repax* and *Nagusta* that were seen were on leaves of trees (especially citrus, mango and *Ficus*), although a few were associated with salticid nest complexes on tree trunks and walls of buildings. *S. repax* and *Nagusta* were occasionally seen standing on or near web silk that often enmeshed vegetation, with this silk especially often being from *Tetragnatha* spp. However, it was considerably more common to find these reduviids on or near salticid nests and nest complexes. For both species, it was easy to distinguish between adults and nymphs (Fig 11.1). At least to the human eye, the nymphs of *Nagusta*, being pale in colour, were especially effectively camouflaged when standing on salticid silk. The impression from seeing these two species in the field was that, most of the time, when they were seen, they were standing on or within a few millimetres of a salticid nest complex. Occasionally they were standing on or within a few millimetres of a solitary salticid nest. Almost always the nest or nest complex was on a leaf, although occasionally the bugs were associated with nest complexes on walls of buildings or tree trunks. *Nagusta* was especially prone to be standing on or next to salticid nest silk, but *S. repax* tended to be somewhat more likely to be found on a leaf as much as a centimetre from salticid nest silk or on a leaf on which there was no salticid nest silk at all. It was also routine to see cast-off exoskeletons of *Nagusta* on salticid nest silk, either with or without the bugs also being present (Fig 11.2).

Nagusta was often found in the company of other conspecific individuals on nests and nest complexes (Fig 11.3). Group size and composition was highly variable (i.e., any combination of the two sexes of adults and the different size classes of nymphs might be present together, and group size ranged from 2 to as many as a dozen or more, with smaller groups being more common). When seen, *S. repax* tended to be either the only reduviid present, except that occasionally *S. repax* was on nest complexes at which *Nagusta* was also present.

The most common occupants of the complexes with which *S. repax* and *Nagusta* were associated were *Menemerus* sp. A, *Pseudicius* sp. A and *Pseudicius* sp. B. A limited census (Table 11.1 and 11.2) of the location of bugs in an area dominated by citrus and *Ficus* trees was consistent with the qualitative impressions.

Predatory Behaviour of Scipinnia repax

Scipinnia repax was seen in the field feeding on a wide variety of prey, including insects (bugs, caterpillars, lake flies and mosquitoes), web-building spiders (especially *Tetragnatha*) and salticids (including *Myrmarachne melanotarsa*, *Pseudicius* spp., *Menemerus* spp, and various other species that have not been identified). The bugs on which *S. repax* was observed feeding included *Nagusta*, normally with *S. repax* standing on salticid nest silk while feeding. In the laboratory, *S. repax* readily preyed on all of the arthropods from the field prey records and on others, including termites. However, it was never seen eating ants, and actively avoided coming close to ants when observed in the laboratory. Yet *S. repax* readily preyed on *M. melanotarsa* and other species of *Myrmarachne* in the laboratory.

Before attacking, *S. repax*'s initial response was usually to move its two antennae up and down, touching the prey on the down stroke ('antennating'). Down strokes were not very forceful. Amplitude and speed varied considerably, but tended to be 2-3 mm at about two strokes per second.

S. repax's typical prey-capture behaviour was to lunge suddenly at the prey (i.e., by extending its legs, the bug moved its body rapidly forward and forcefully contacted, and held on to, the prey). *S. repax*'s forelegs went over the prey, and then flexed back, bringing the prey closer to the bug's body. The bug then inserted its proboscis into the prey. *S. repax* occasionally inserted its proboscis first into the prey's abdomen or its legs, but initial insertion was more often in the head or anterior thorax of an insect or in the anterior cephalothorax of a spider. The prey was slow to succumb when initial insertion was in a leg or the abdomen, sometimes taking 10 min or longer before becoming completely quiescent. However, prey usually became

quiescent after a few seconds when initial insertion of the proboscis was in the prey's head, anterior thorax or the anterior cephalothorax.

Sometimes *S. repax*'s prey-capture technique was somewhat different when the prey was a salticid. While being antennated by *S. repax*, salticids typically did not appear to be very alarmed. Usually the salticid simply walked away from the reduviid at an ordinary, or not particularly fast, pace. *S. repax* typically followed, continuing to antennate and repeatedly extending its proboscis, and inserted its proboscis in the abdomen of the salticid while the salticid walked. When the salticid that was walking away was large (in body length, more than about $\frac{1}{4}$ the body length of the bug), and regardless of size when it was walking fast, the bug usually attacked by lunging. However the bug often inserted its proboscis without lunging when the salticid that was walking away was small and moving slowly. When the bug attacked from behind, it generally elevated its body before inserting the proboscis, managing in this way to insert its proboscis in the salticid's cephalothorax.

In the field, *S. repax* was sometimes seen standing with its proboscis inserted through the silk on a salticid's nest and into a salticid or a salticid's eggs inside the nest. In this way, the bug stood outside the nest while feed on a salticid or a salticid's eggs that were inside. At night in the laboratory, *S. repax* walked on to salticid nests and then became quiescent. The duration of the quiescent period was highly variable, sometimes lasting for 60 min or longer. Eventually, *S. repax* pushed its proboscis slowly through the silk and slowly probed about inside. If a salticid or a salticid's eggs were contacted, the bug inserted its proboscis by making a sudden, forceful thrust downward. If unsuccessful at contacting a salticid or salticid eggs, or unsuccessful at impaling the salticid after contact, the bug withdrew its proboscis from the silk and became quiescent again. Intermittently, the bug took a few steps or pivoted about, changing its position on the nest. Usually the salticid remained in the nest and eventually the bug re-inserted its proboscis and tried again from another location on the nest.

When feeding on an egg, the bug left its proboscis in one place until finished. Otherwise, what happened next depended on the part of the prey's body the bug's proboscis had been inserted into. If already in the head of an insect or the anterior cephalothorax of a spider, the bug kept its proboscis in place. Otherwise, once the prey became quiescent, the bug removed its proboscis and re-inserted it into the insect's head or the spider's anterior cephalothorax. After several minutes, however, the bug began shifting the position of its proboscis frequently. During this time, *S. repax* tended to concentrate especially on feeding from various locations on the prey's antennae and legs.

Scipinnia repax occasionally fed on prey as large or slightly larger than itself. Most of its prey, however, were about half the bug's size in body length. Two or more individuals of *S. repax* were never seen sharing prey.

Predatory Behaviour of Nagusta

In general, *Nagusta* was a more sluggish reduviid compared with *S. repax*, rarely moving very fast even if poked with a finger or a pair of forceps. However, *Nagusta* made rapid lunging attacks similar to those made by *S. repax*. Before making an attack, it was typical for *Nagusta* to be quiescent, with the sudden lunge at the prey being preceded by little or no antennating or other preliminary contact. If it failed to make a capture when it lunged, *Nagusta* rarely followed its prey. Once the prey became quiescent, *Nagusta*'s feeding routine was similar to that of *S. repax* (shifting proboscis into the insect's head or the spider's anterior cephalothorax, and then, after feeding for a few minutes, frequent shifting of proboscis positioning). However, in contrast to *S. repax*, *Nagusta* concentrated on positioning its proboscis in the prey's abdomen.

The prey *Nagusta* was seen feeding on in the field, and the prey it readily attacked in the laboratory, were distinctively small compared with the prey of *S. repax* (in body length, generally about 1/10th the size of *Nagusta*). In typical prey-capture sequences, *Nagusta* rested facing the door of a salticid's nest (or chamber in a nest complex) and made a sudden attack on

a salticid that was entering or leaving. *Nagusta* also attacked small salticids that were walking about on the surface of the nest silk or the leaf. Most of the time, *Nagusta* remained quiescent while the salticid walked about, sometimes touching or even walking on top of *Nagusta*, without provoking a reaction or at most stimulating *Nagusta* to adjust its posture or step slightly to the side. Once a small salticid was positioned directly in front, *Nagusta* sometimes, without apparent warning, lunged and made a capture. Small juveniles of *Portia africana* are among the prey *Nagusta* was seen feeding on in the field, and *Nagusta* readily preyed on small juveniles of *P. africana* in the laboratory. As a regular visitor to salticid nest complexes, opportunities for *Nagusta* to prey on *P. africana* may be common.

In the field, *Nagusta* was seen feeding on lake flies and especially salticids (Fig 11.4 & Fig. 11.5). Often *Nagusta* was seen resting on nests with salticid eggs inside. However, *Nagusta* was never seen in the field or the lab pushing its proboscis through nest silk to feed on eggs, although it did readily eat salticid eggs if the silk was first pulled away with forceps. However, *Nagusta* appeared to be especially predisposed to waiting on the silk of salticid nests containing eggs (Fig 11.6) and young juveniles (Fig 11.7), capturing the juveniles as they emerged from the nest.

Recently hatched spiderlings of *Tetragnatha* sp. were also preyed on by *Nagusta*. *Tetragnatha* females sit with their eggsacs on masses of stray webbing that cover leaves and other vegetation, and the *Tetragnatha* juveniles disperse into the webbing after emerging from the eggsacs. *Nagusta* sometimes moved into the webbing, and ate the juveniles.

DISCUSSION

Although most reduviid species may be generalist predators, there also appear to be some remarkable examples of specialisation. There are, for example, scattered reports in the literature on ant-reduviid relationships. *Ptilocerus ochraceus*, for example, is a reduviid that associates, sometimes in large numbers with particular ants, *Dolichoderus bituberculatus* (Jacobson 1911), and preys on the ants. *Acanthaspis* is another reduviid genus known for

preying on ants: *Acanthaspis quinquespinosa* (Pruthi 1947), *A. concinnula* (Mühlenberg and Maschwitz 1976), and *A. pedestris* (Vijayavathi 1987). *Acanthaspis* has also been reported to prey on termites (Odhiambo 1958). *Salyavata variegata* (McMahan 1982) and *Lisarda* (Miller 1956) appear to be reduviids that specialise on termites. Reduviids from the subfamily Ectrichodiinae appear to be obligate predators of millipedes (Louis 1974), and *Phonoctonus fasciatus* appears to specialise especially narrowly, perhaps exclusively, on cotton stainers and related species from the heteropteran *Pyrrhocoridae* (Kirkpatrick 1957, R.R. Jackson, unpublished data).

Specialisation by reduviids on spiders has also been reported. Species from the genus *Stenolemus* in the reduviid subfamily Emesinae inhabit spider webs (Howard 1901, Smith 1910, Wickham 1910, Dicker 1941, Usinger 1941, Brown and Lollis 1963, Wygodzinsky 1966). It has been suggested that *Stenolemus lanipes* may feed almost exclusively on the web-building spider *Achaearanea tepidariorum* (Snoddy *et al.* 1976), and predation on spiders may be a genus-wide characteristic of *Stenolemus* (Cobben 1978). These bugs have distinctive, slender bodies and long legs that may have morphological adaptations that help them move about freely in spider webs (Schuh and Slater 1995).

Scipinnia repax and *Nagusta* may, like *Stenolemus*, be predators that target especially spiders as prey, but with a difference. The prey of *S. repax* and *Nagusta* seem especially often to be salticids. Although neither of these two reduviids feeds exclusively on salticids, this preliminary study suggests that salticids might be preferred prey. *S. repax* appears to take a wider range of prey than *Nagusta*, including taking *Nagusta* itself as prey. Perhaps with *S. repax* we may have found a reduviid that singles out as preferred prey not only salticids but also salticid-eating reduviids. *Nagusta* may, in turn, prey often on a predator of salticids, another salticid, *Portia africana*.



Fig 11.1. *Nagusta* sp. adult (left) and two nymphs (right).



Fig 11.2. Cast-off exoskeletons of *Nagusta* on salticid nest silk



Fig 11.3. *Nagusta* sp. adults and nymphs clustered on a leaf.



Fig 11.4. *Nagusta* sp. nymph eating *Menemerus* sp. B (Salticidae)



Fig 11. 5. *Nagusta* adult eating *Pseudicius* sp. A (Salticidae)

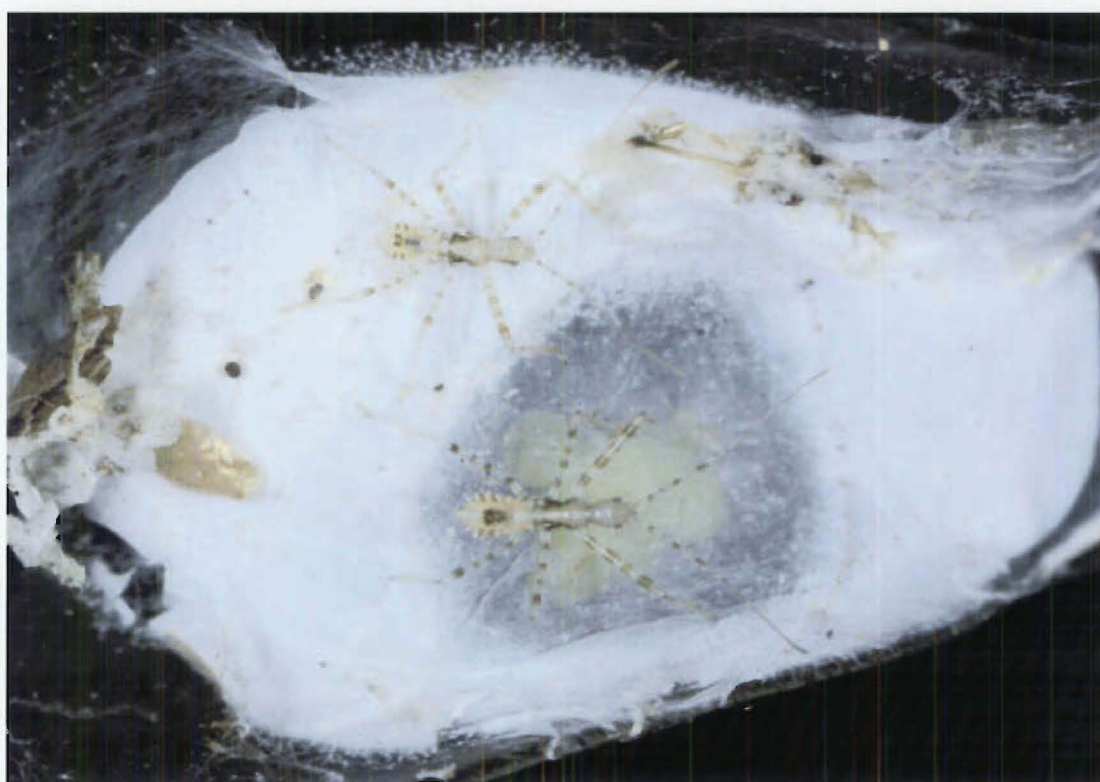


Fig 11. 6. *Nagusta* nymphs on a salticid nest containing eggs.



Fig 11.7. *Nagusta* nymph (left) and adult (right) on salticid nest with juvenile of *Portia africana* (Salticidae) also on nest (top).

Table 11.1. Location of *Scipinnia repax* during a census of tree leaves (primarily citrus and *Ficus*)

	On or within a few mm of salticid nest complex	On or within a few mm of solo salticid nest	On leaf with salticid nest or nest complex >5 mm away	On leaf with no salticid nest or nest complex present on the same leaf
No other reduviids present	5	1	3	1
One or more other <i>S. repax</i> present	0	0	0	0
Two or more <i>Nagusta</i> , but no other <i>S. repax</i> , present	2	0	0	0

Table 11. 2. Location of *Nagusta* sp. during a census of tree leaves (primarily citrus and *Ficus*)

	On or within a few mm of salticid nest complex	On or within a few mm of solo salticid nest	On leaf with salticid nest or nest complex >5 mm away	On leaf with no salticid nest or nest complex present on the same leaf
No other <i>Nagusta</i> present	9	2	1	0
One or more other <i>Nagusta</i> present	34	4	0	0

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Chapter 12

Bugs that eat spiders and bugs that eat spider-eating bugs: prey-choice behaviour of *Nagusta* sp. and *Scipinnia repax*.

Abstract

Previous work has shown that *Nagusta* sp. and *Scipinnia repax*, assassin bugs from East Africa, prey on salticid spiders, and *S. repax* also preys on *Nagusta* sp. Here the prey-choice behaviour of both species is investigated experimentally in the laboratory. Simultaneous-presentation testing was carried out with lures pushed slowly in front of the predators. Both species chose salticid spiders more often than they chose other prey. *S. repax* chose *Nagusta* more often than it chose other insects and also more often than it chose salticids. Methods used in this, the first extensive experimental study of the prey-choice behaviour of reduviids, are potentially applicable to many other predatory insects.

INTRODUCTION

In an earlier study (Chapter 11), *Nagusta* sp. and *Scipinnia repax*, assassin bugs (Reduviidae) from East Africa, were shown to prey especially often on salticid spiders in the field, and *S. repax* also preyed on *Nagusta* sp. These observations suggested hypotheses about prey preferences. Conceptually, a predator's choices and preferences are distinct from its actual diet in nature (Morse 1980, Li and Jackson 1996; Cross and Jackson in press) because 'choice' refers to perceptual and decision-making processes and 'preference' refers to the predator's attitude toward different types of prey (the salience of the prey type to the predator), whereas 'diet' refers to what the predator actually eats. Although diet may be influenced by preference, it may also be influenced by active prey defence, prey availability, and other factors. Conclusions about a predator's preferences require evidence from experiments designed to test perception and decision making. Here, after developing appropriate experimental design, I investigate the preferences of *Nagusta* sp. and *S. repax*.

MATERIALS AND METHODS

All experiments were based on simultaneous-presentation testing using lures. However, the methods used in many studies on the prey-choice behaviour of salticid spiders had to be modified. Salticids readily respond from a distance to motionless lures made from dead prey mounted on cork disks in lifelike posture (see Chapter 7), but the reduviids showed little or no response to lures prior to contact. A device ('fork') was designed for bringing two prey individuals simultaneously into contact with the bug being tests (Fig 12.1).

The fork was a plastic block (the 'handle') with an attached rigid wire (the 'stem') (length 50 mm). At the opposite end of the stem, there were two fine insect pins ('prongs' of the fork) (length 20 mm), each glued to an end of a horizontal stiff wire (length 10 mm) that was in turn glued centred on the end of the stem.

To begin a test, the two lures were slowly pushed between the test bug's two front legs so that they came simultaneously into contact with bases of the bug's two antennae. In successful tests, the reduviid grasped one of the two lures with its front legs. Testing was terminated whenever a test bug moved before contact was made and whenever simultaneous contact of the two lures with the bug's antennae could not be achieved.

The arthropods used for lures were collected at Mbita Point from the same habitat as the reduviids. Here the objective was to provide the reduviid with tactile and potentially chemical cues, whereas the intention in Chapter 7 had been to limit the salticid to using only optical cues. This meant that, when making lures, the methods were somewhat different from in Chapter 7. Specimens were not put in ethanol and they were not glued to cork discs. Each lure was made by first killing the spider or insect by asphyxiation using carbon dioxide. Next it was tethered to one of the prongs on the fork (i.e., the pin was pushed into the posterior abdomen of the dead arthropod). The dead insect was always used in a test about 60 min after asphyxiation. The lure was always

positioned right-side-up and facing directly forward from the fork. No specimens that were noticeably damaged were used.

Three prey species were used for making lures (Table 12.1). In each instance, the prey was 4 mm in body length: *Nagusta* sp. (juvenile) (used with *S. repax* only); a salticid, *Menemerus* sp. A (adult female); a lake fly (Diptera, Chironomidae), *Nilodorum brevibucca*. *Nagusta* was tested with lake flies and salticids as prey. *S. repax* was tested with each pair-wise combination of the three prey species. The reduviid tested was always a juvenile that was 10 mm in body length.

RESULTS

Nagusta chose the salticids significantly more than they chose lake flies (Table 12.2, $\chi^2=9.091$, $P<0.01$), as did *S. repax* (Table 12.2, $\chi^2=10.89$, $P<0.01$). *S. repax* chose *Nagusta* significantly more often than salticids (Table 12.2, $\chi^2=7.364$, $P<0.05$) and significantly more often than lake flies (Table 12.2, $\chi^2=21.125$, $P<0.001$).

DISCUSSION

Being predators with exceptionally good eyesight, salticids can be readily be tested with motionless lures presented from a distance and there have been numerous experimental studies illustrating the prey-choice behaviour of these particular predators. Comparable experimental studies on most predatory insects are scarce. This has been the first extensive experimental investigation of the prey-choice behaviour of any reduviids, and it required modifying the testing procedure used with salticids. By contacting the predator simultaneously with two different lures, the prey choices of *S. repax* and *Nagusta* were determined. These testing methods are likely to be applicable to other reduviids, as well as many other predatory arthropods.

Now that an effective method has been derived for prey-choice testing of these two reduviids, a wider range of prey should be used. However, the findings reported here, although limited to using three prey species suggests some preliminary conclusions.

‘Araneophagic reduviids’ appears to be an appropriate label for *S. repax* and *Nagusta*, as they both feed frequently on salticids in the field and, in prey-choice tests, they chose salticids more often than they chose lake flies. Salticids, especially the social salticids that live in nest complexes, are very abundant in the habitats of these two species, and it appears that, as especially abundant prey, they have become the target of predators that specialize on them as prey. These reduviids prey primarily on small salticids (Chapter 11), and it may be primarily the smallest active stages (the recently-hatched juveniles) on which these reduviids most often prey. The social salticids at Mbita Point are not only small but also extremely common, and it is probably on these species that *S. repax* and *Nagusta* most often prey in nature.

Nagusta is especially abundant on salticid nest complexes, often with groups of conspecific individuals clustering on the same nest complex and sometimes even feeding together on the same individual prey. It is interesting that this especially abundant reduviid seems to have become an opportunity for an additional layer of preference in the other araneophagic reduviid, *S. repax*. With *S. repax*, we appear to have found a reduviid that singles out salticids as preferred prey and then goes a step further and singles out *Nagusta*, another salticid-specialist reduviid, as most preferred prey of all.

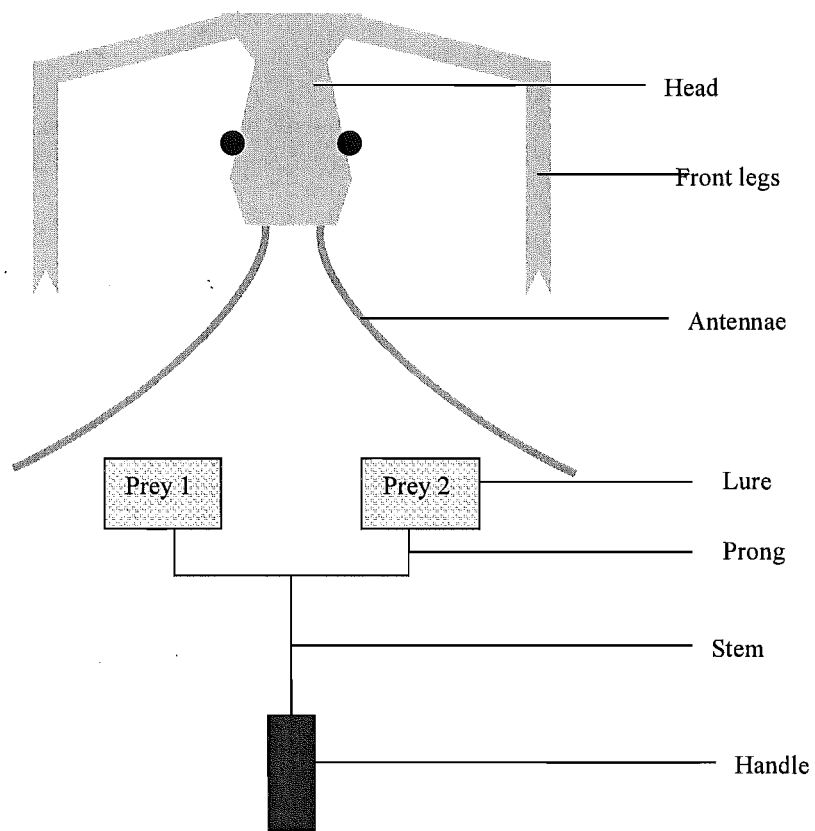


Fig 12. 1. Reduviid being presented simultaneously with two types of prey. Prey: lures, made from dead arthropods, tethered to pin (prong on a ‘fork’). See text for details.

Table 12.1. Arthropods used as prey (lures). Prey choice testing of *Nagusta* sp. And *Scipinnia repax*.

Description	Species	Order and family	Body length of specimens used (mm)
Midge	<i>Nilodorum brevibucca</i>	Diptera, Chironomidae	4.0
Salticid	<i>Menemerus</i> sp. A	Araneae, Salticidae	4.0
Assassin bug	<i>Nagusta</i> sp.	Hemiptera, Reduviidae	4.0

Table 12.2. Simultaneous-presentation testing of two reduviid species. Prey: lures made from dead arthropods pushed into contact with reduviid. Comparison: Chi square test for goodness of fit (null hypothesis: 50/50).

Reduviid tested	Prey 1	Prey 2	Chose Prey 1	Chose Prey 2	Comparison
<i>Nagusta</i> sp.	Salticid	Midge	11	1	$\chi^2= 9.091$, $P<0.01$
<i>Scipinnia repax</i>	Salticid	Midge	16	2	$\chi^2= 10.889$, $P<0.01$
	<i>Nagusta</i>	Midge	29	3	$\chi^2= 21.125$, $P<0.001$
	<i>Nagusta</i>	Salticid	31	13	$\chi^2= 7.364$, $P<0.05$

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Chapter 13

How social salticids defend against predation by salticid-eating assassin bugs

Abstract

Menemerus sp. A, *Pseudicius* sp. A, and *Pseudicius* sp. B. are social jumping spiders (Salticidae) from East Africa that normally live in nest complexes. *Scipinnia repax* is an assassin bug (Reduviidae) that specialises in preying on these salticids. In an experimental study, the defensive role of the salticids' nests and nest complexes was investigated. The reduviid more readily captured solitary salticids that had no nests than solitary salticids that were in solitary nests. The reduviid also more readily captured salticids that were in solitary nests than salticids clustered in nest complexes.

INTRODUCTION

Salticid nests have been likened to a fortress (Jackson 1976), a silk barrier that many potential predators have difficulty breaching. Nests may also be envisaged as something akin to a burglar alarm, because active predators inadvertently send early-warning signals across the silk to the resident salticid (Jackson and Pollard 1996). However, salticid nests are neither impregnable fortresses nor foolproof alarms. For example, both *Portia fimbriata*, an araneophagic salticid from Queensland, Australia (Jackson and Blest 1982), and *Taieria erebus*, an araneophagic gnaphosid spider from New Zealand (Jarman and Jackson 1986) are predators that specialise at preying on nesting salticids.

Menemerus sp. A, *Pseudicius* sp. A, and *Pseudicius* sp. B. are social jumping spiders (Salticidae) from East Africa. Their nest complexes are especially abundant at Mbita Point in western Kenya. *Scipinnia repax* and *Nagusta* sp. are assassin bugs (Reduviidae) that specialise at preying on salticids. Both of these reduviids are common on and near the nest complexes of *Menemerus* sp. A, *Pseudicius* sp. A, and *Pseudicius* sp. B. (Chapter 11), and both have a

preference for salticids as prey (Chapter 12), with *S. repax* having an additional preference for *Nagusta* as prey. *S. repax* tends to be a more active predator than *Nagusta*. When salticids walk away, *S. repax* actively pursues them, whereas *Nagusta* relies primarily on ambushing salticids as they go in and out of their nests. *S. repax* also preys on salticids that are inside nests by pushing its proboscis through the silk (Chapter 11).

The hypothesis I investigate here is that nests and especially nest complexes help protect salticids from attacks by salticid-eating reduviids.

MATERIALS AND METHODS

Experiments were carried out using *S. repax*, the more active of the two predators. In all instances, adult females of *Menemerus* sp. A, *Pseudicius* sp. A, and *Pseudicius* sp. B were tested with adult females. Tests began when an individual *S. repax* was placed in the test cage with a salticid. The cage was then left overnight in the dark. The following morning, the test outcome was a record of whether the salticids had survived.

For tests with salticids with no nest at all (N=127), a single salticid was placed inside an empty cage immediately before testing (*Menemerus* sp. A, N=37; *Pseudicius* sp. A, N=42; *Pseudicius* sp. B, N=48). For tests with salticids in a solo nest (N=126), a single salticid was placed in a cage and left overnight, and it was used the following day if it was inside a nest it had built when it was time for the test to begin (*Menemerus* sp. A, N= 46; *Pseudicius* sp.A, N=41; *Pseudicius* sp. B, N=39). For tests with salticids in nest complexes (N=103), five conspecific salticids were placed within a cage and allowed to build a nest complex overnight (not used if the salticids were not all inside a single nest complex the following morning), and then all but one of these salticids (chosen arbitrarily) were removed before the test began (*Menemerus* sp. A, N=34; *Pseudicius* sp. A, N=35; *Pseudicius* sp. B, N=34).

Results were analyzed using chi square tests of independence, with Bonferonni adjustments when multiple comparisons were made with the same data sets. Data were pooled across salticid species within any one data set because there were no significant differences among the species ($P>0.01$ in all instances).

RESULTS

Mortality was significantly higher among salticids without nests than among salticids with solo nests ($\chi^2 = 16.74$, $P<0.001$) and significantly higher among salticids with solo nests than salticids with nest complexes ($\chi^2 = 9.29$, $P<0.01$ with Bonferroni adjustment) (Fig 13.1).

DISCUSSION

Nests and nest complexes were not 100% effective protection from predation by *S. repax*. The salticid still had to come out of the nest from time to time, and *S. repax* can also prey on salticids that are inside nests by penetrating the silk with its proboscis. However, having a nest appears to make a difference, providing the salticid with a partial barrier against the attacks of this predator. While solo nest may provide a protective barrier, a nest complex seems to be even better. One factor may be that the silk walls of the nest complexes are more difficult for the reduviid to penetrate. Another factor may be how a nest complex forms something like a maze, giving the salticid multiple entry and exit points (i.e., more alternatives for how to go in and out of nests without getting dangerously close to the predator).

The general conclusion suggested by these findings is that nest complexes function for salticids largely as mechanisms for anti-predator defence. Additional studies are needed. Whether the findings with *S. repax* can be replicated with *Nagusta* is an obvious next step. When *Nagusta* is the predator, the maze effect may be particularly important because *Nagusta* tends to ambush salticids as they come and go from the nest, and *Nagusta* has not been seen penetrating nests with its

proboscis. It will also be important in future studies to ascertain whether, and how, nest complexes might defend salticids against other predators besides reduviids. For example, the maze effect may also be important in defence against *Portia* juveniles that make predatory raids on nest complexes. It will be especially interesting to see how nest complexes might help defend against raiding ants, as ants seem to be the most abundant potential predators in the environments of these salticids.

Having found evidence that a nest complex may be safer than a solo nest, it will be interesting to determine whether bigger nest complexes are safer than smaller complexes. There may be a point beyond which adding more nests to complexes does not significantly add to anti-predator efficacy. If there are also disadvantages to living in nest complexes, then it might be that the size of nest complexes in given environments reflects tradeoffs, with larger nest complexes being the norm in environments where the reduviids, or other comparable predators, are more numerous.

It is interesting that *S. repax* and *Nagusta* appear to prey primarily on small to very small salticids, and the social salticids tend to be especially small species. Perhaps these two reduviid species have been an especially important selection pressure favouring nest-complex building by the social salticids. For larger salticids, defence against these reduviids may not be so important, which may help explain why larger salticids tend not to form nest complexes.

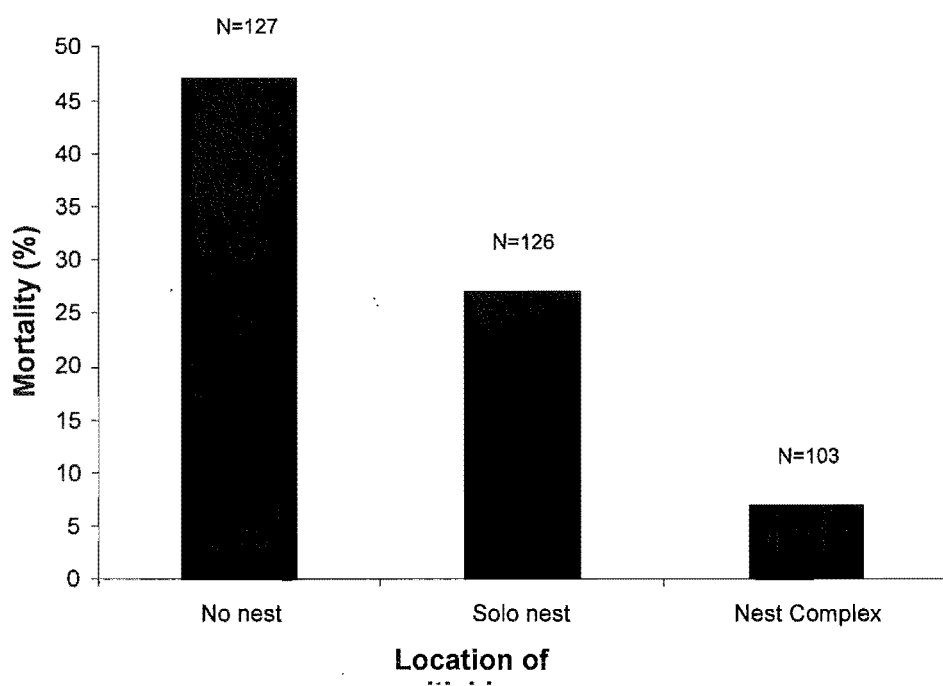


Fig 13.1. Influence of presence of solo nest or nest complex on percentage of salticids (pooled data: *Menemerus* sp. A, *Pseudicius* sp. A and *Pseudicius* sp. B) when left in presence of *Scipinnia repax*

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Chapter 14

Joining Decisions of Social Salticids.

Abstract

Using seven saltcid species from East Africa that, in the field, live in nest complexes ('social salticids'), laboratory experiments were carried out to clarify the joining decisions responsible for nest-complex formation. All seven species were shown to make joining decisions, but the different species varied in the details of their decision rules. Comparable experiments were carried out on a more typical saltcid species (i.e., a species that does not normally live in nest complexes), and this species was shown to be averse to joining. Experimental findings show that the salticids make their decision on the basis of cues from the silk of the other salticids and cues from seeing other saltcid individuals.

INTRODUCTION

Seven East African saltcid species have been shown to live routinely in nest complexes (Chapter 2) that vary considerably in physical size, the number of occupants, and the identity (sex, age class, species) of the occupants. *Parajotus cinereus* was usually found only in single-species groups. The other species (*Menemerus* sp. A, *Menemerus* sp. B, *Menemerus* sp. C, *Pseudicius* sp. A, *Pseudicius* sp. B, *Myrmarachne melanotarsa*) were often found in mixed-species complexes. Six of these species were also found sometimes in solo nests, but *Myrmarachne melanotarsa* was always in nest complexes, usually with other species. These findings suggest that different species may make different joining decisions. This chapter is a first step toward investigating these joining decisions.

In studies of social spider groups, the propensity of individuals to join one another has traditionally been termed 'interattraction'. However, this word has problematical implications when studying the joining decisions of individuals because 'inter' in 'interattraction' implies that the outcome of an interattraction test is the result of two individuals having mutual, if not equal, urges to join one another. However, the conclusions

supported by data from ‘interattraction studies’ generally are not this strong. When tests are conducted with two living individuals in each other’s company, the outcome is a product of each individual acting and reacting. As the individuals involved may not all be motivated in the same way, it might often be more appropriate to view the outcome as compromise between two individuals with different motivation rather than as evidence of mutually arrived-at decisions.

In this chapter, the objective is to clarify how the joining decisions made by salticids might account for the origin of nest complexes. My central hypothesis is that the social salticids end up sharing nest complexes because they actively seek each other out and decide to join. My experiments are designed to clarify the decision rules of the salticids and the cues that govern these rules.

METHODS

General

Eight salticid species from East Africa were studied. Besides the seven species that were routinely found living in nest complexes (Chapter 2: *Menemerus* sp. A, *Menemerus* sp. B, *Menemerus* sp. C, *Pseudicius* sp. A, *Pseudicius* sp. B, *Myrmarachne melanotarsa*, and *Parajotus cinereus*), I also used *Plexippus* sp., a species that is not typically found in nest complexes (i.e., *Plexippus* served as an example of a ‘typical’ solitary salticid). Comparing data from testing other species with data from testing *Plexippus* served as a basis for determining whether the social salticids adopted special joining decisions.

The salticids were collected from the field at the Thomas Odhiambo Campus of the International Centre of Insect Physiology and Ecology (Mbita Point, Kenya), and then tested in the laboratory. Standard laboratory procedures were adopted (see Jackson and Hallas 1986). The laboratory photoperiod (L:D) was 12h:12h, with lights being switched on at 0700h.

All salticids that were used were adult females. The testing apparatus was a central clear plastic tube (120 mm long x 10 mm in diameter) with a transparent vial (40 mm long x 10 mm in diameter) at each end. The tube had a small hole (5 mm in diameter) half way along its

length, plugged with a cork. The cork was removed for introducing the spider into the tube and then replaced. Between tests, tubes and vials were cleaned with 80% ethanol followed by distilled water.

There were five test series. For series 1-4, each vial was covered by a removable, but tight-fitting, black paper sheath (Fig. 14.1). For test series 5, the apparatus was modified by the addition of a plastic pot at each end of the tube, with the vial at each end being glued to the centre of the inside of the pot. The vial was not covered with a paper sheath. The pot was 50 mm diameter at the wider (open) end and 40 mm at the narrow (closed) end to which the vial was glued. The distance from the wide to the narrow end was 35 mm.

Test Series 1. Choice between empty vial and vial containing nest of another salticid

At 1200 hours, adult female salticids from all of the test species were placed in vials (one per vial) and left overnight (vials not connected to tube). The salticid was then removed from the vial at 0700 hours the next morning. The vial was used only if the salticid had built a nest in the vial. The nest-containing vial was connected to one end of the tube (left or right decided at random) and a clean vial was connected to the other end of the tube. A second salticid (the 'test spider') was introduced at 0800 hours into the tube, and it was then left until 0700 hours the following morning, when the sheaths were removed from the vials and the location of the test spider and any additional nests were recorded.

Test spiders tended to settle in the dark sheath-covered vial instead of the tube. When, in rare instances, a salticid settled in the tube, the test was aborted. Using this criterion for a successful test, there were two basic results: the test spider 'joined' (i.e., settled in the same vial as the other salticid's nest) or it did not join (i.e., it settled in the opposite vial). Adult females were tested with silk from both conspecific and non-conspecific individuals.

Test Series 2. Choice between solo nest built by a conspecific individual or a nest complex built by four conspecific individuals

Methods were as for Series 1 except that in each test one of the two vials contained a nest complex consisting of four nests. The nest complex was obtained by leaving four, instead of one, salticids in a single vial overnight and using the vial only if a four-chamber nest complex was built.

Test Series 3. Choice between a solo nest built by a conspecific individual and a nest complex built by four non-conspecific individuals

Methods were as for Series 2 except that the individual that built the nest complex were not conspecific with the test spiders.

Test Series 4. Choice between a nest complex built by four conspecific individuals and a nest complex built by four non-conspecific individuals.

Methods were as for Series 2 and 3 except that both vials contained nest complexes. One vial had a complex built by conspecific adult females and the other had a nest complex built by non-conspecific adult females.

Test Series 5. Influence of seeing conspecific and non-conspecific individuals on choice of nest complex to join.

Methods were as for Series 4 except for the different apparatus, the presence of mounts and having in each vial a nest complex built by four conspecific adult females. There were mounts in one pot (conspecific or non-conspecific salticids) and the other pot remained empty.

Mounts were made using standard techniques (Chapters 4, 7, and 8), and four mounts were glued evenly spaced around the vial on the inside of each pot (spaced so that each was midway along the length of the vial).

Data analysis

Chi-square tests of goodness of fit were used (null hypothesis: 50% settle in test vial and 50% settle in control vial for all tests). When $p < 0.05$, the findings from the tests are referred to as 'significant joining' or 'significant avoidance'. Further data analysis was carried out using chi-square tests of independence.

RESULTS

Test Series 1. Choice between empty vial and vial containing nest of another salticid

Menemerus sp. A, *Menemerus* sp. B, *Pseudicius* sp. A, *Pseudicius* sp. B, and *M. melanotarsa*, but not *Menemerus* sp. C and *Plexippus* sp., settled significantly more often in the vial with silk than in the control (no silk) vial (Fig. 14.2). *P. cinereus* settled significantly more often in the vial with the conspecific nest, but there were no significant trends when tested with other types of silk.

Data from all testing of *P. cinereus* with nests built by non-conspecific individuals were pooled and then compared with data from testing *P. cinereus* with nests built by conspecific individuals. There were significantly more tests in which *P. cinereus* chose the vial containing the nest when the nest was built by a conspecific than chose the vial containing the nest when the nest was built by a non-conspecific individual (test of independence, $P < 0.001$).

Test Series 2. Choice between solo nest built by a conspecific individual or a nest complex built by four conspecific individuals

Menemerus sp. A, *Menemerus* sp. B, *Pseudicius* sp. A, *Pseudicius* sp. B, *M. melanotarsa*, and *P. cinereus* (Fig 14.3) significantly more often chose nest complexes instead of solo nests.

Test Series 3. Choice between a solo nest built by a conspecific individual and a nest complex built by four non-conspecific individuals

Menemerus sp. A, *Menemerus* sp. B, *Menemerus* sp. C, *Pseudicius* sp. A, *Pseudicius* sp. B, and *M. melanotarsa* chose non-conspecific nest complexes significantly more often than solo conspecific nests (Fig 14.4). There were, however, no significant differences in how often *P. cinereus* chose nest complexes and chose solo nests.

Test series 4. Choice between a nest complex built by four conspecific individuals and a nest complex built by four non-conspecific individuals.

Parajotus cinereus chose nest complexes built by conspecific individuals significantly more often than nest complexes built by non-conspecific individuals. For each of the other species tested, there was no significant difference in how often conspecific and non-conspecific nests were chosen (Fig 14.5) by any of the species tested.

Test series 5. Influence of seeing conspecific and non-conspecific individuals on choice of nest complex to join.

Menemerus sp. A, *Menemerus* sp. B, *Pseudicius* sp. A, *Pseudicius* sp. B, *M. melanotarsa*, and *P. cinereus* settled significantly more often in the vials that were surrounded by mounts made from conspecific individuals than in vials not surrounded by mounts (Fig 14.6). There was no significant difference in how often *Menemerus* sp. C settled in one or the other vial.

In tests with non-conspecific mounts (Fig 14.6), all species showed significant preference for settling in the vials with *Menemerus* sp. A mounts except for *P. cinereus*, which showed significant aversion to vials with *Menemerus* sp. A mounts.

Significant preference for settling in vials with *Menemerus* sp. B mounts was shown by *Menemerus* sp. A, *Pseudicius* sp. A, and *M. melanotarsa*. *Menemerus* sp. C showed no

significant preference for vials with *Menemerus* sp. B mounts, and *P. cinereus* showed significant aversion to vials surrounded by non-conspecific mounts.

Significant aversion to vials surrounded by *Menemerus* sp. C mounts was evident for all the species tested (*Menemerus* sp. A, *Menemerus* sp. B, *Pseudicius* sp. A, and *Pseudicius* sp. B).

Significant preference for vials surrounded by *Pseudicius* sp. A was shown by *Menemerus* sp. A, *Menemerus* sp. B, *Pseudicius* sp. B, and *M. melanotarsa*. *Menemerus* sp. C showed no significant preference for vials surrounded by *Pseudicius* sp. A mounts. *P. cinereus* showed an aversion to vials surrounded by these mounts.

DISCUSSION

Joining decisions

Joining with one another is part of what it means for animals to form groups. However, the extent to which joining is brought about by individual animals making active decisions can not be determined simply by observations. Experimental evidence is needed for ruling out the logical possibility that individuals remain more or less oblivious to the presence of other individuals and yet end up clustered (i.e., for ruling out that clustering might come about without individuals responding directly to each other). Individual animals may, for example, form a group solely because of responding to the physical environment in the same way, rather than to each other. The experimental findings in this chapter, however, suggest East African social salticids detect cues pertaining to the presence of other salticids and base joining decisions on these cues, with different decision rules ('joining strategies') apparently being adopted by the different species.

Active joining strategies have received considerable attention in the literature on social spiders, but primarily under the term 'interattraction'. As commonly used, this term refers to situations in which spiders form groups at least partly because individuals in the group are

attracted to each other. 'Interattraction' has been defined variously as an intrinsic 'urge for associating' (Kullman 1972), a 'propensity to aggregate' (Downes, 1994), responding to an 'intraspecific, sex-independent, attracting stimulus' (Lindauer 1974), or an 'inner drive leading to sociality' (Stern and Kullman 1975). Although not necessarily part of the term's formal definition, there is a tradition of envisaging interattraction as applying specifically to conspecific individuals (i.e. interattraction is typically envisaged as a mechanism for bringing conspecific individuals together).

Sometimes the use of particular terms may predispose researchers towards particular questions, and I eventually became disillusioned with how the term 'interattraction' seems to channel questions about social spiders. One factor was realizing that the species I studied required going against the tradition of 'interattraction' being used in the context of individuals belonging to the same species. Even more problematic may be how 'inter' in the term 'interattraction' suggests that joining is a joint decision by two or more individuals (i.e., something to which they mutually agree). This term seems to inhibit considering the possibility that individuals make different joining decisions and still end up together. The methods and data that are often cited when the term 'interattraction' is used do not generally support precisely the interpretations suggested by the term. It is as if the term itself creates a momentum to extend interpretation of findings beyond what the methods used and the data presented actually support. For this reason, I became disillusioned with the term 'interattraction' and decided to use terms that make it easier to consider each individual's decisions separately.

It is more straightforward to use the term 'settling' for when an animal comes to rest in a particular location in its environment and 'joining' specifically for when an individual settles close to another individual. Unlike the term 'interattraction', these terms ('settling' and 'joining') do not imply particular answers to the question of why individuals settle in particular places or decide to join other individuals. In this chapter, 'joining' meant more specifically settling close to or in or on the nests of other individuals.

Not only do the terms ‘settle’ and ‘join’ make it easier to ask old questions in a new way. They also make it easier to appreciate that different individuals in a group may be using different decision rules. The terms ‘settling’ and ‘joining’ are more compatible with investigating group formation as a consequence of habitat selection (see Stamps 1988, Stamps 1991, Monkkonen et al 1999), where other animals are a part of the habitat, and there is less temptation with those words to envisage same-species groups as being automatically more relevant than multi-species groups for understanding sociality.

There is literature on multi-species groups in vertebrates, and this literature is perhaps more instructive for understanding sociality in spiders, or at least salticid spiders, than the better known (to arachnologists) literature on eusociality in insects (Wilson 1971). One problem is that eusociality is defined in a way that pertains exclusively to single-species groups, whereas the social salticids appear to have more in common with multi-species vertebrate groups. In vertebrate groups, one species sometimes has a more active role in maintaining an association, the other species being more passive. Mixed-species groups of black-and-white colobus monkeys (*Colobus guereza*) and red colobus monkeys (*Procolobus tephrosceles*) are examples. The red colobus often follows the black-and-white colobus when the group travels, but not the other way around (Chapman and Chapman 2000). Social salticids may provide additional examples of one species actively seeking out and joining with other species, but with the joined species tolerating the companion species rather than actively encouraging its efforts to join. In particular, *M. melanotarsa* appears to be a salticid species that actively maintains associations with other salticids that may try to avoid these ant-mimic salticids but eventually tolerate their presence.

Finding animals that routinely live in groups raises questions concerning the potential benefits the individual animal might gain from the association. One of the most frequently acknowledged hypothesis concerning benefits for social predators is that individuals in a group can share prey. However, the traditional use of the term ‘share’ in the spider literature is

revealing. Typically, when two or more individuals of the same spider species feed together on the same prey item, they are said to be ‘sharing’ prey and they are often called ‘social spiders’ largely on this basis. Yet there are well-known examples of two or more individuals belonging to different species feeding together on the same prey. Numerous species from the theridiid genus *Argyroides*, for example, routinely feed alongside araneid and tetragnathid species (Cangialosi 1990, Tso and Severinghaus 2000, Miyashita 2001), but the conventional term used for what *Argyroides* does is ‘kleptoparasitism’ rather than ‘sharing’, and the tradition has not been to call the group consisting of *Argyroides* plus the araneids or tetragnathids a ‘group of social spiders’. My impression, as a result of studying East African salticids, is that ‘sharing’ and ‘kleptoparasitism’ may be useful expressions for ends of a continuum, but that these are not qualitatively different categories of behaviour.

Settling on Silk

Silk from salticids and from other spiders is a common part of the habitat of the species I studied, with the salticids in the field often being found in nest complexes embossed in the silk of web-building spiders (Chapter 2). Silk may be a feature of the habitat that matters to the salticids in a direct way (e.g., as a shelter from environmental stresses (excessive water, high temperature, and so forth), as a fortress for defence against some of the salticid’s predators, or as a support to which to attach its own nest). Silk might also be a cue that indicates to the salticid that other salticids are in the vicinity. Perhaps settling in a habitat already occupied by other salticids is advantageous because of direct benefits that will be derived from being in the presence of the other salticids. The presence of other salticids may also be an indicator of the good quality of the habitat, independent of any direct benefits from being in the company of the other salticids. Settling on silk has been documented for a number of other spider species (Buskirk 1975, Krafft and Roland 1979, Jackson 1982, Roland 1983, Seibt and Wickler 1988,

Evans and Main 1993), suggesting that silk is generally an important element in reinforcing group cohesion in social spiders (Darchen 1965).

The different species of East African salticids studied here appear to make different joining decisions depending on the cues presented to them. The presence of nest silk for most of the social salticid species appears to trigger settling. In most cases, this silk does not have to be from a conspecific to trigger settling although certain species seem to be choosier about this than others. For example, in test series 1 and 4, *P. cinereus* settled on silk from conspecific individuals, but not on silk from other salticid species. However, in test series 3, where the choice was between a solo nest built by a conspecific individual and next complex built by non-conspecific individuals, *P. cinereus* showed no preference. The ultimate cause of *P. cinereus* being species-specific in its silk choice when choosing between two solo nests or two nest complexes, the apparent overriding of this specificity when the choice is between a solo nest and a nest complex, is unknown, but these findings suggest that the benefits of grouping for *P. cinereus* are specifically linked to grouping with conspecifics, whereas in the other species this may not be the case.

Settling on silk appears to be a feature of the social salticid species that encourages grouping and provides a proximate explanation for why the social-salticid species are found in nest complexes. Why they have this tendency in the first place, though, is a question about ultimate causation for which we have no clear answer. However, a predilection to settle on silk is not simply a universal feature of salticid biology. As a control, a generally solitary salticid species, *Plexippus* sp., was tested in the same way as the social salticids and the presence of silk had no did significant effect on the settling decisions of *Plexippus* sp.

Spider Size and Joining Decisions

In the literature on spider sociality, there are numerous examples of spider species in which juveniles, but not adults, form groups (Avilés and Gelsey 1998, Pourié and Trabalon

1999, Johannessen and Lubin 2001). Compared with adults, juveniles are different in a number of ways, including being at an earlier stage of development. However, one of the simplest differences is that juveniles tend to be smaller than adults in body size.

For the experiments reported in this chapter, I used only adults, as a comparison of adults with juveniles would have made an already-large chapter even larger. For the social-salticid species tested, both adults and juveniles were found living in nest complexes in the field. However, it is interesting that the adults of the social-salticid species tended to be in body size small relative to most salticids. Of the salticids I used in experiments, *Plexippus* sp. and *Menemerus* sp. C were the largest in body length and they were the species for which the tendency to join was least pronounced. *Plexippus* was chosen deliberately as a representative non-social salticid, but *Menemerus* sp. C is often found in nest complexes in nature.

The influence of body size on the joining decisions of salticids will need to be examined in detail in future studies, but an initial hypothesis can be suggested. For all salticids, some kind of cost-benefit analysis is probably appropriate for understanding the joining decisions of individuals, and the cost-benefit function may often be tipped to the benefit side when the salticids are small. For example, smaller salticids may be more vulnerable to ants, reduviids, and other predatory arthropods, suggesting that living in a nest complex may benefit these smaller salticids more than it may benefit larger salticids. Investigating this interesting hypothesis was beyond the scope of this thesis.

Visually Determined Joining Decisions

It was of particular interest to determine whether the joining decisions of social salticids were influenced by seeing other salticids in the vicinity because most spiders appear to have only rudimentary eyesight, but salticids have unique, complex eyes and visual acuity unsurpassed by any other animals in their size range. By using stationary mounts, movement and olfactory cues were ruled out. Evidently, on the basis of optical cues, *Menemerus* sp. C

chooses to settle at nest complexes if sees other conspecific individuals in the vicinity but seeing individuals of other species has no effect. Other social-salticid species avoided joining nest complexes when individuals of *Menemerus* sp. C were seen in the vicinity, but joined when they saw the other social-salticid species in the vicinity. On the whole, the findings from testing with mounts were similar to findings from testing with silk cues only.

Menemerus sp. C appears not to be influenced by seeing other social-salticid species in the vicinity, but seeing conspecific individuals made it more inclined to join. The other social-salticid species all avoided joining nest complexes surrounded by individuals of *Menemerus* sp. C. *Parajotus cinereus* joined nest complexes when it could see conspecific individuals in the vicinity. *Menemerus* sp. A, *Menemerus* sp. B, *Pseudicius* sp. A, *Pseudicius* sp. B and *Myrmarachne melanotarsa* all joined nest complexes surrounded by other social salticids as long as they were not *Menemerus* sp. C. *Menemerus* sp. C is a large salticid compared with the other nest-inhabiting salticids studied and, in the field, this species has been seen sometimes preying on its smaller neighbors. It might be adaptive for the smaller social salticids to avoid this bigger and more dangerous member of the community.

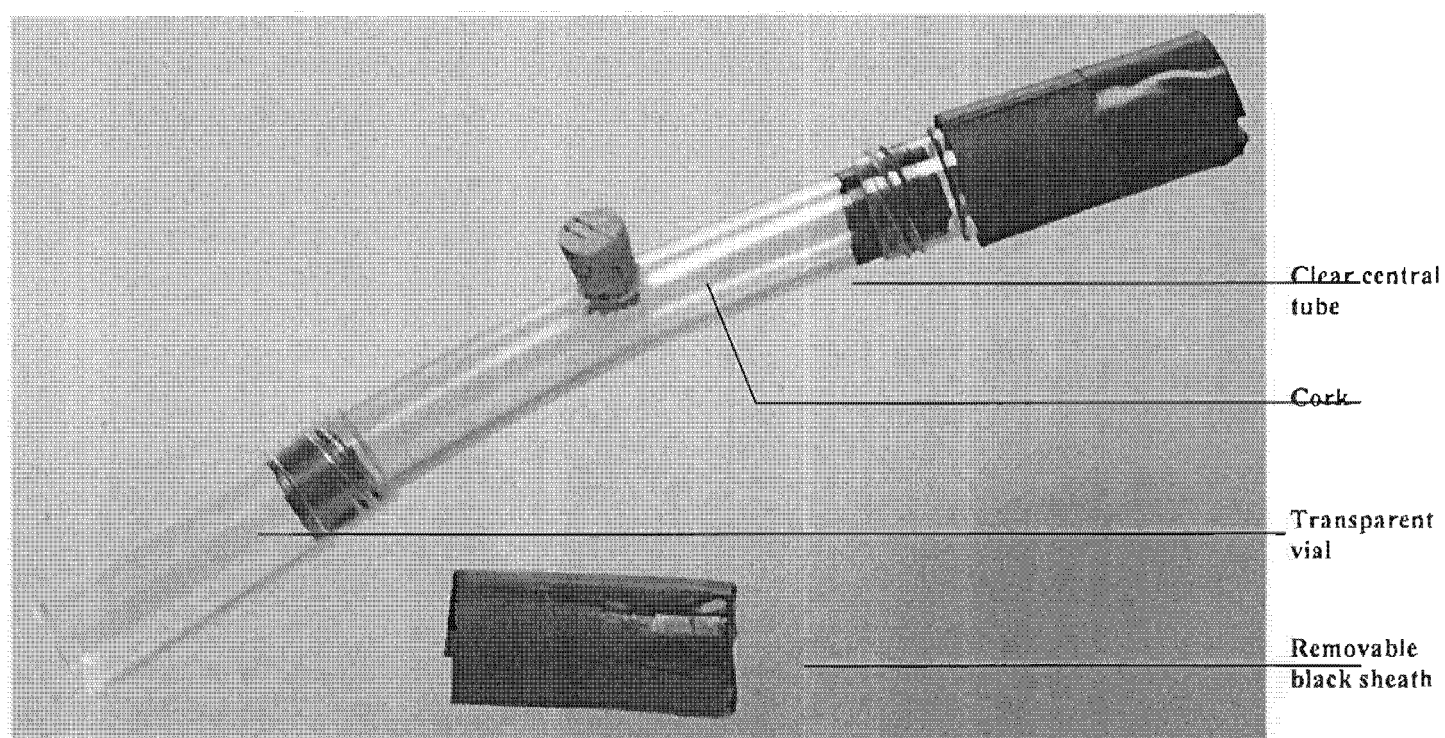
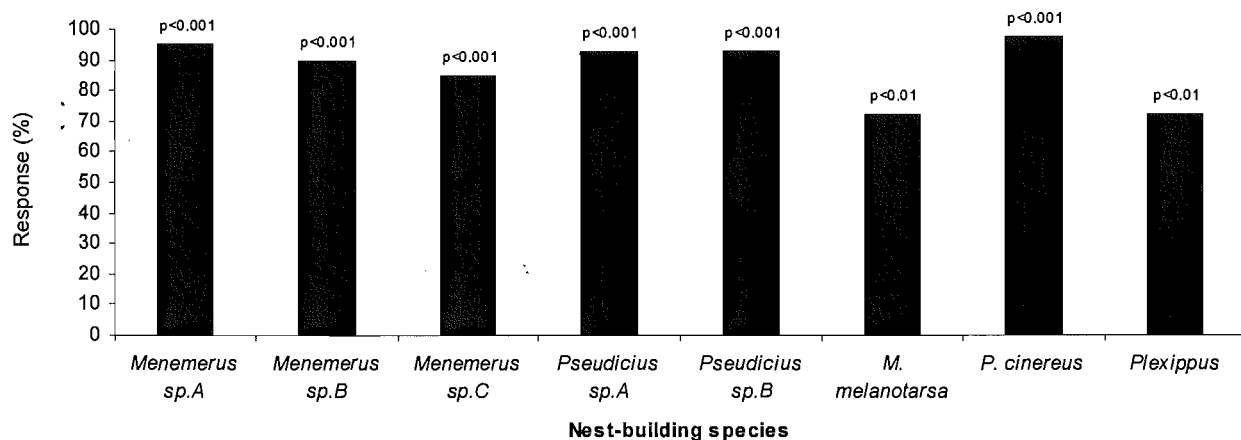


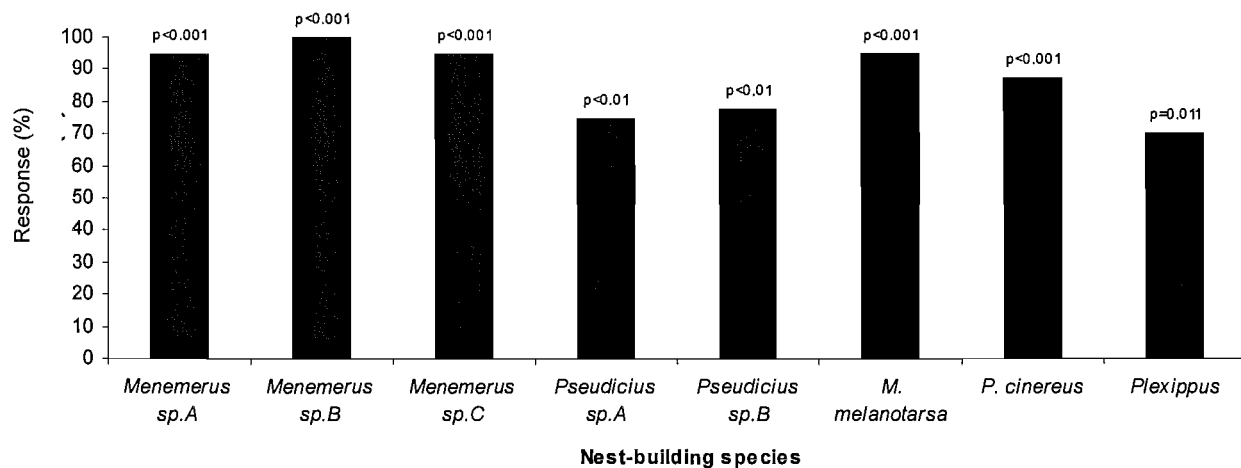
Fig 14.1. Test apparatus. See text for details.

Fig 14.2. Response (settled in vial with nest of another salticid when alternative was a clean vial). See text for details of methods. Test-spider species above histogram. For each type of nest, N=40. No individual test spider and no individual nest-source spider used more than once. Spiders tested were adult females.

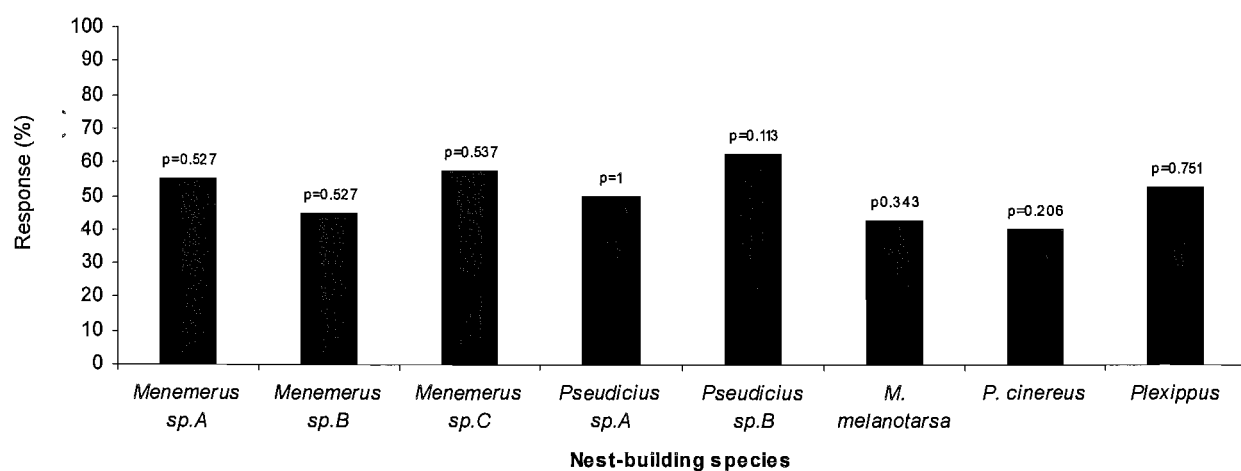
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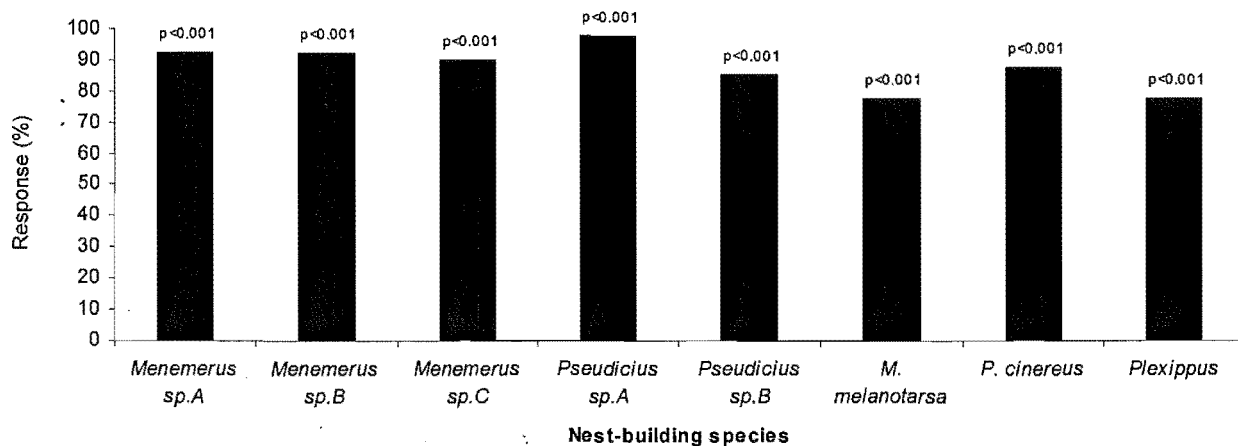
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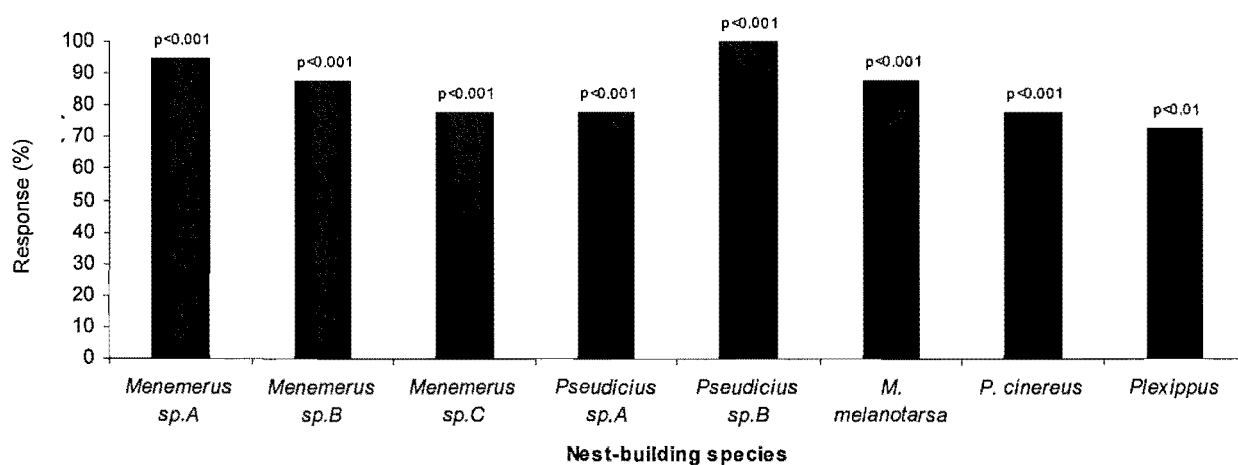
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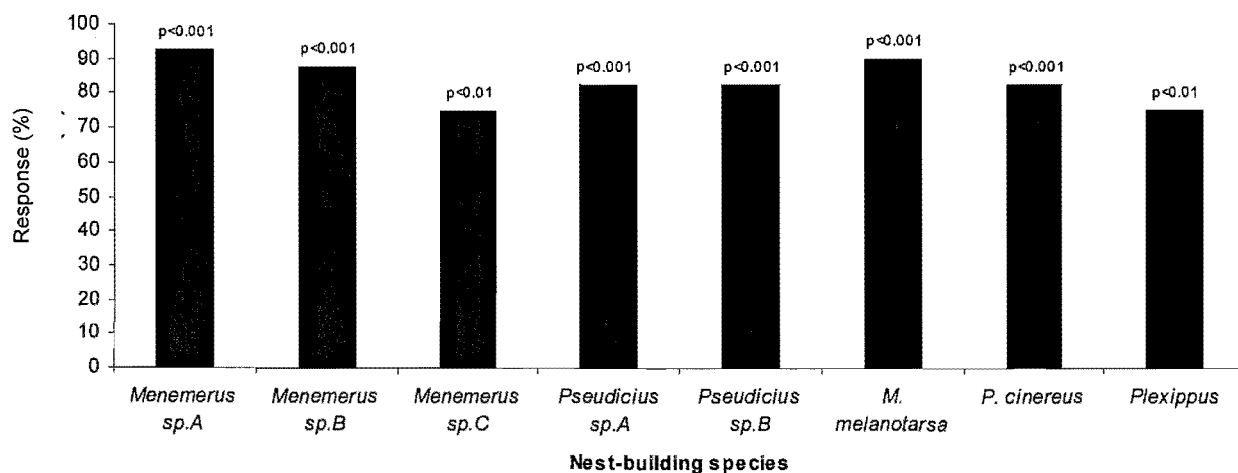
Pseudicius sp. A

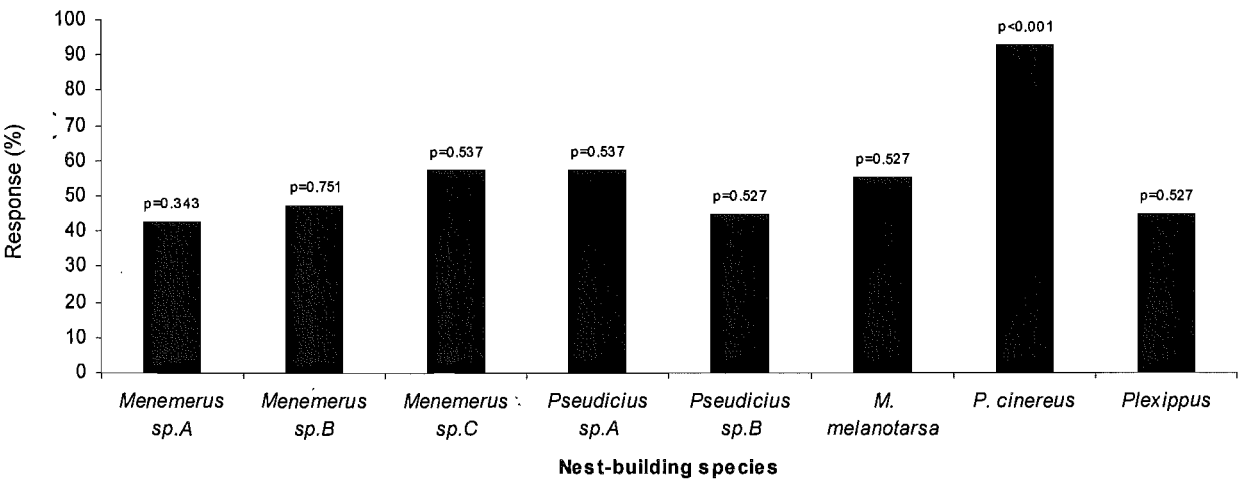


Pseudicius sp. B

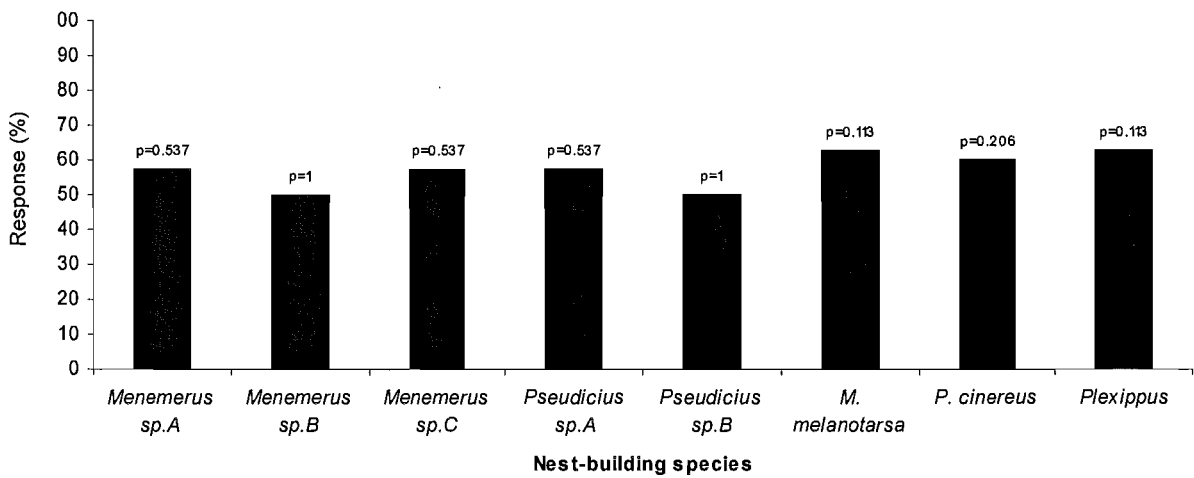


Myrmarachne melanotarsa





Plexippus sp.



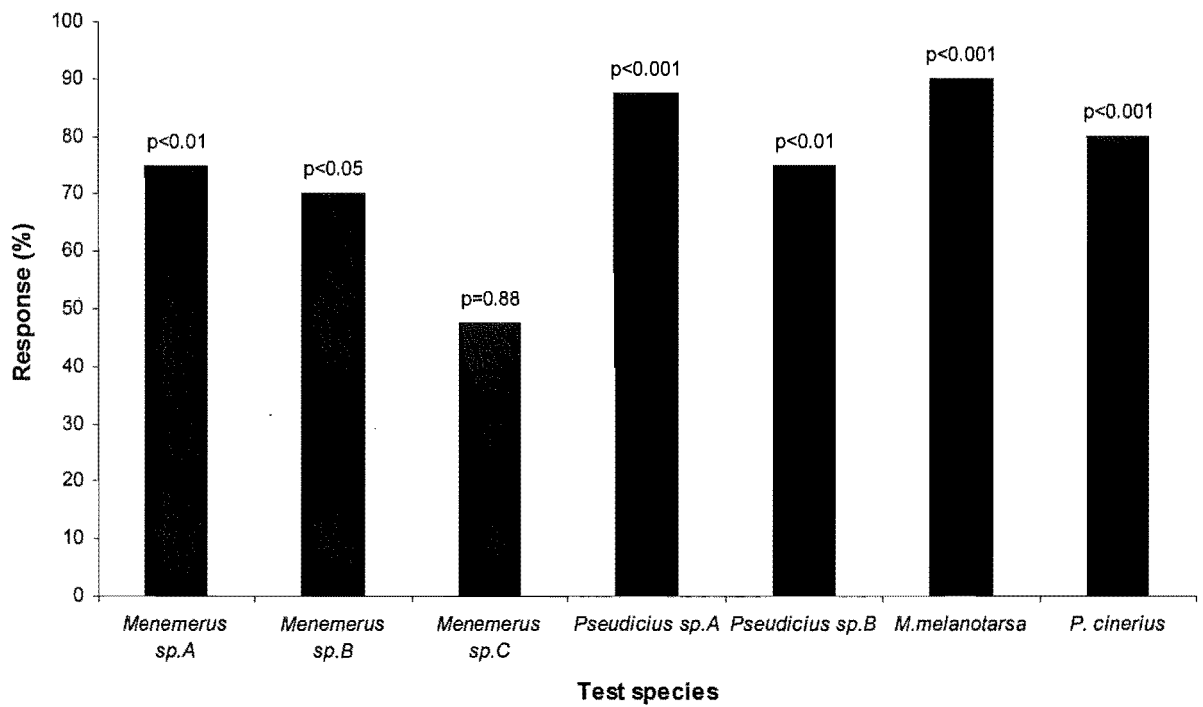


Fig 14.3. Response (settled in vial with nest complex when alternative is single nest). All nests build by individuals conspecific with the test spider. See text for details of methods. For each type of nest, N=40. No individual test spider and no individual nest-source spider used more than once.

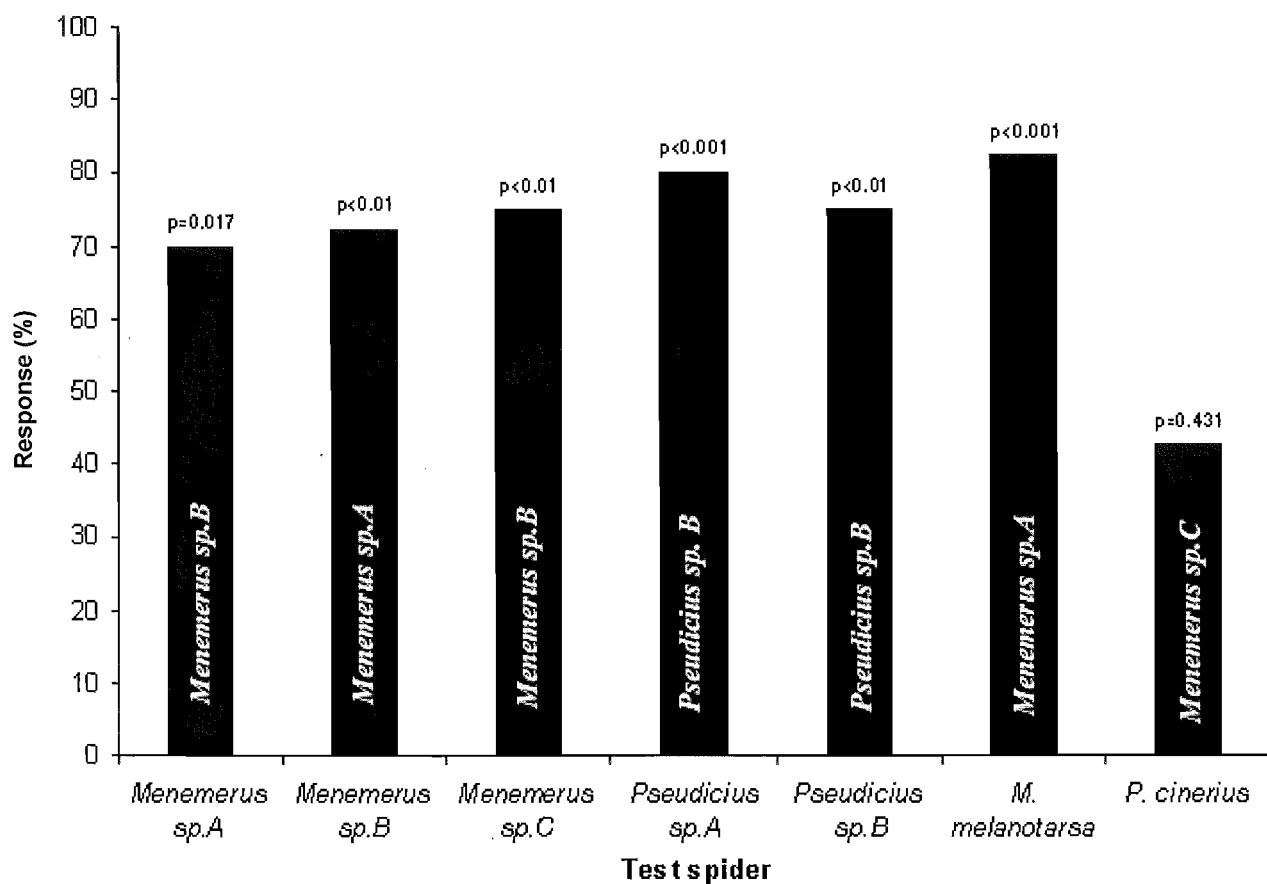
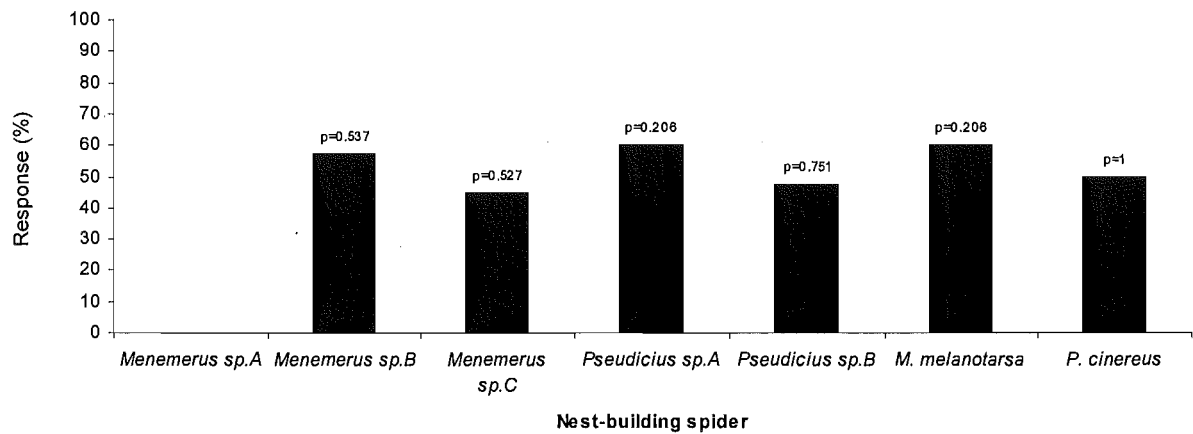


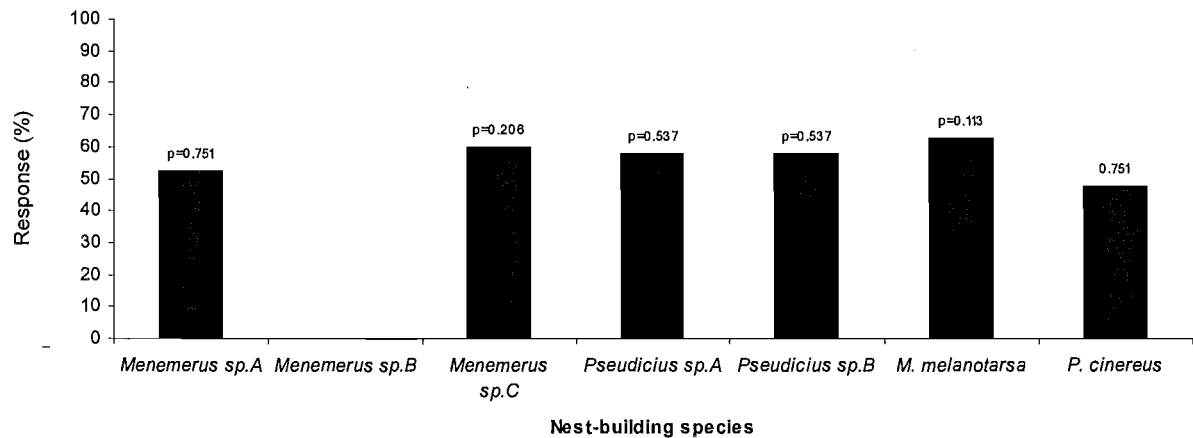
Fig 14.4. Response (settled in vial with nest complex when alternative is single nest). Single nest built by individual conspecific with the test spider. Nest complex built by four individuals not conspecific with test spider (species indicated inside bar). See text for details of methods. For each type of nest complex, N=40. No individual test spider and no individual nest-source spider used more than once.

Fig.14.5. Response (settled in vial with nest complex built by conspecific individuals when alternative was nest complex built by non-conspecific individuals). Each nest complex built by four individuals. See text for details of methods. For each type of nest complex, N=40. No individual test spider and no individual nest-source spider used more than once.

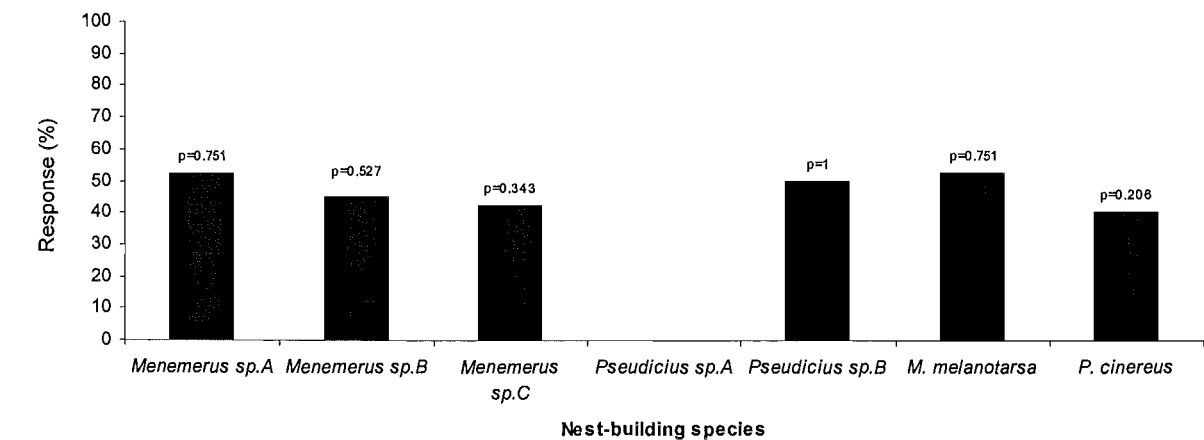
Menemerus sp.A



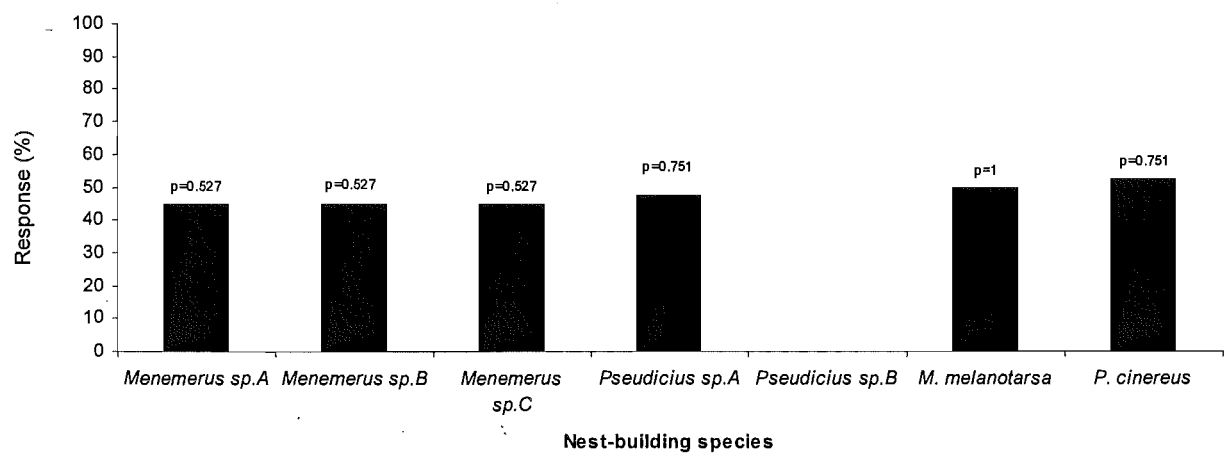
Menemerus sp. B



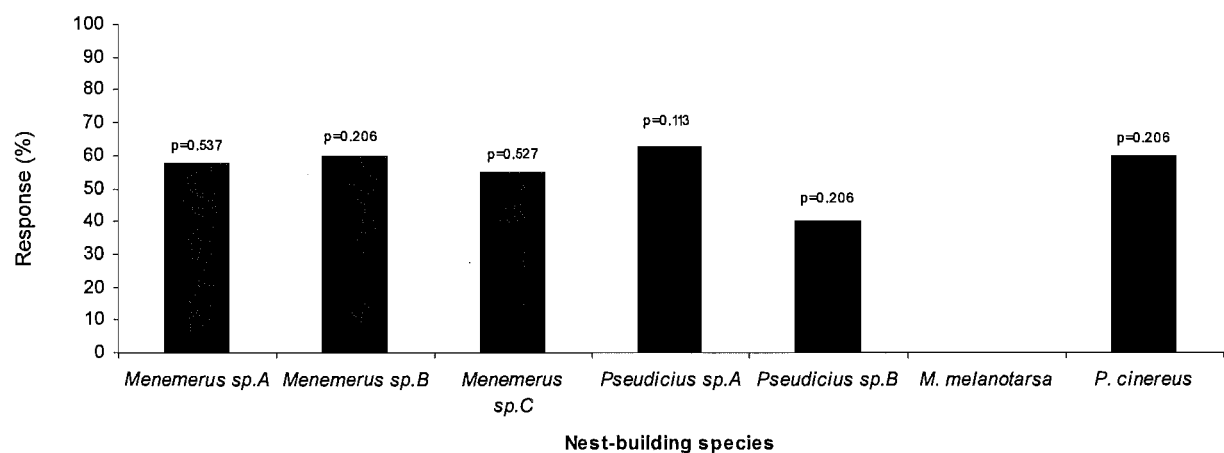
Pseudicius sp. A



Pseudicius sp. B



M. melanotarsa



Parajotus cinereus

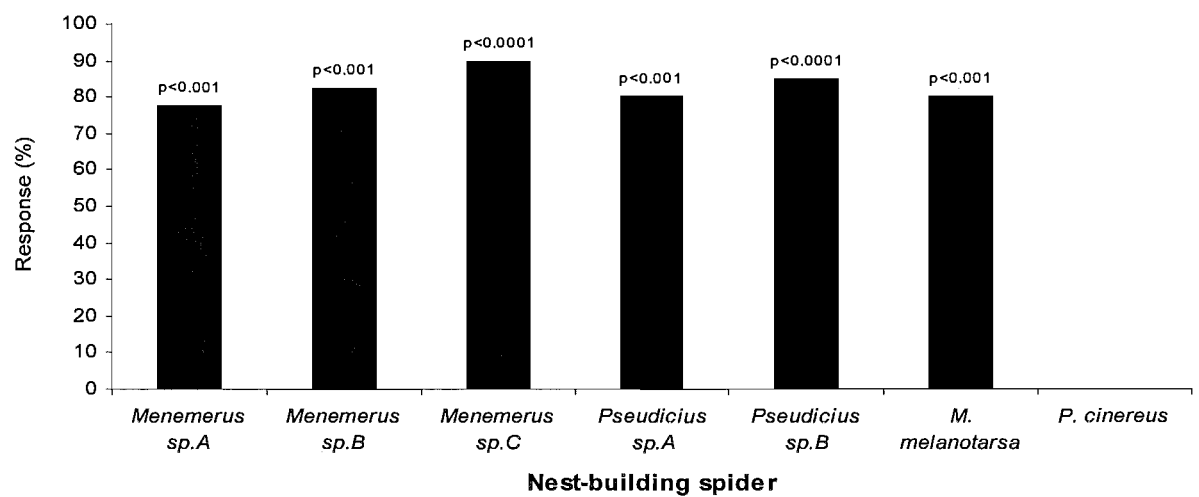
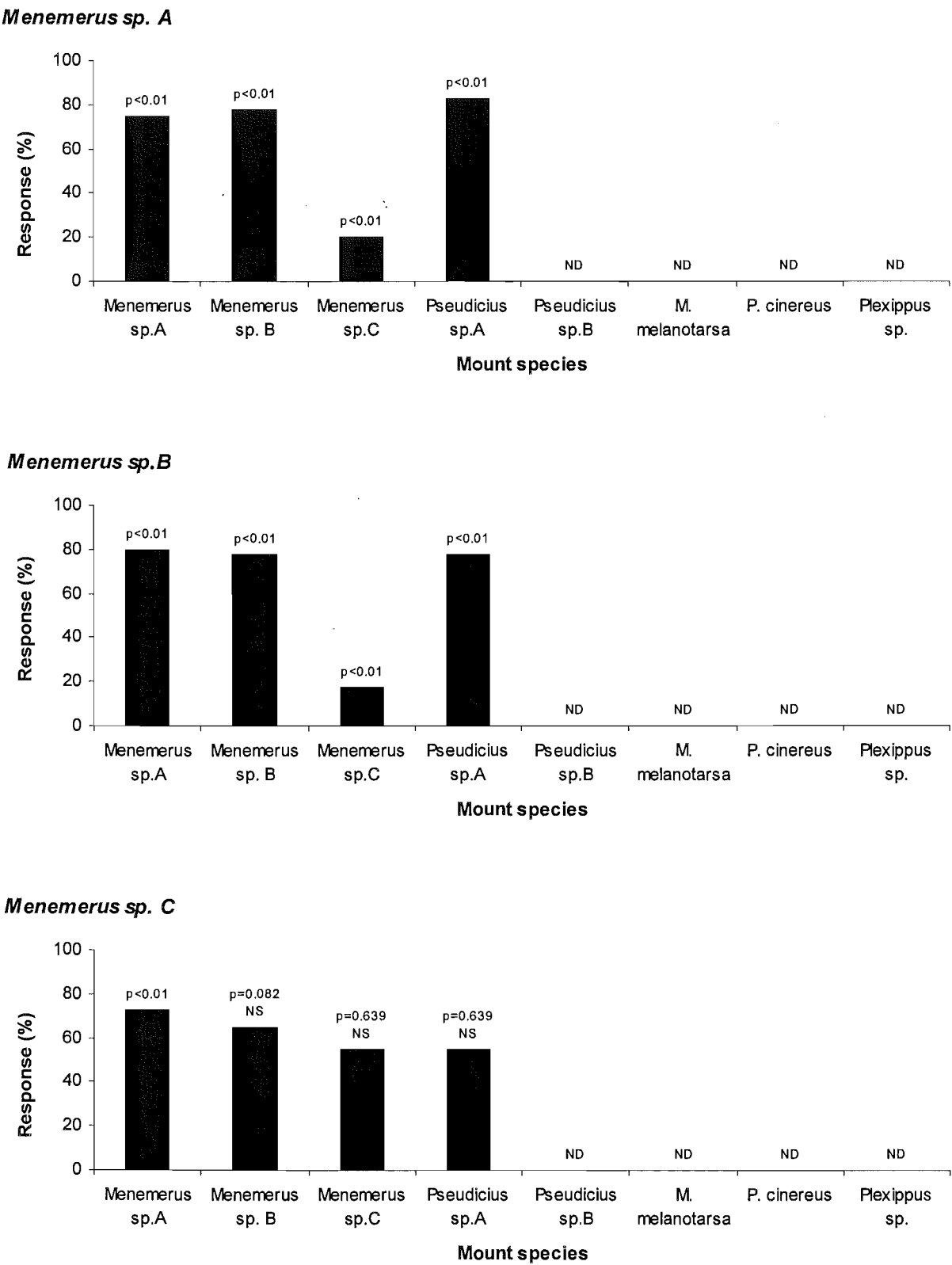
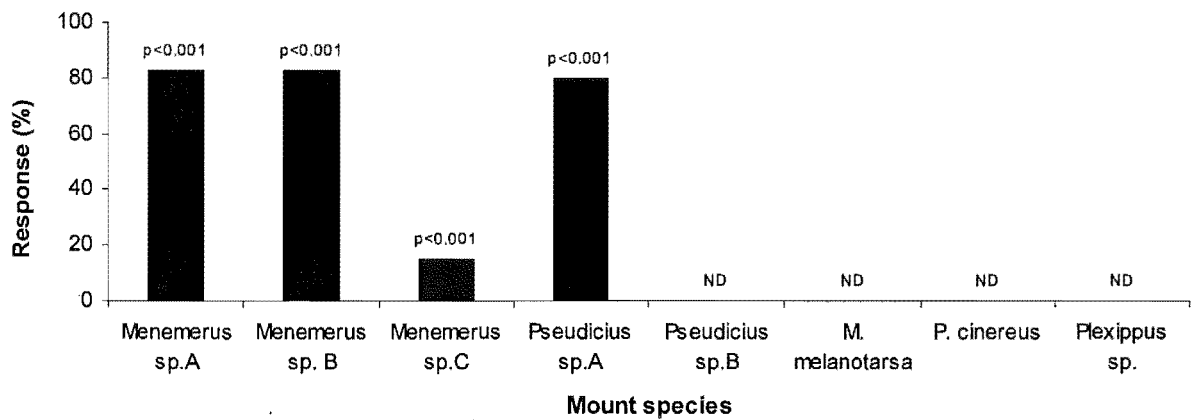


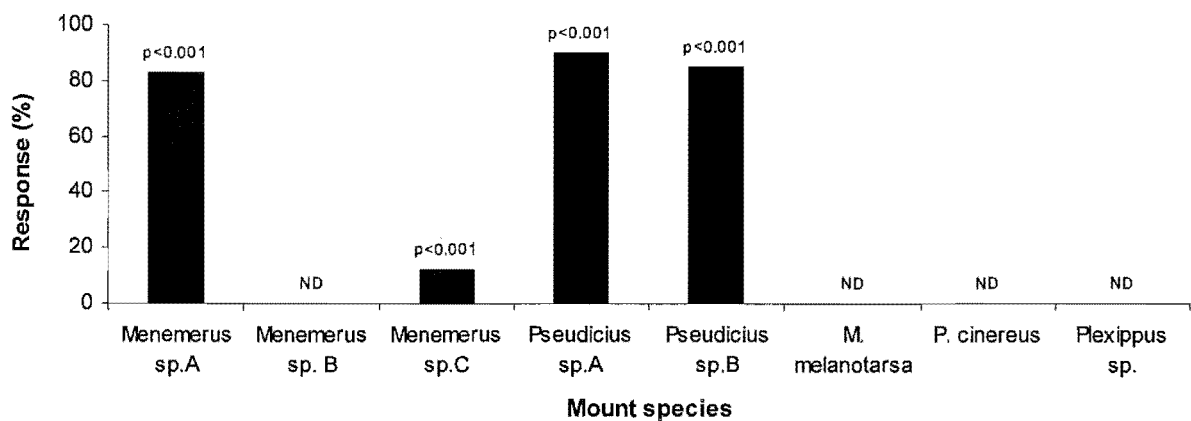
Fig 14.6. Response (settled in vial containing nest complex surrounded by mounts when alternative was nest complex not surrounded by mounts). Nest complexes built by four conspecific individuals. See text for details of methods. For each bar, N=40. No individual test spider, no individual mount and no individual nest-source spider used more than once.



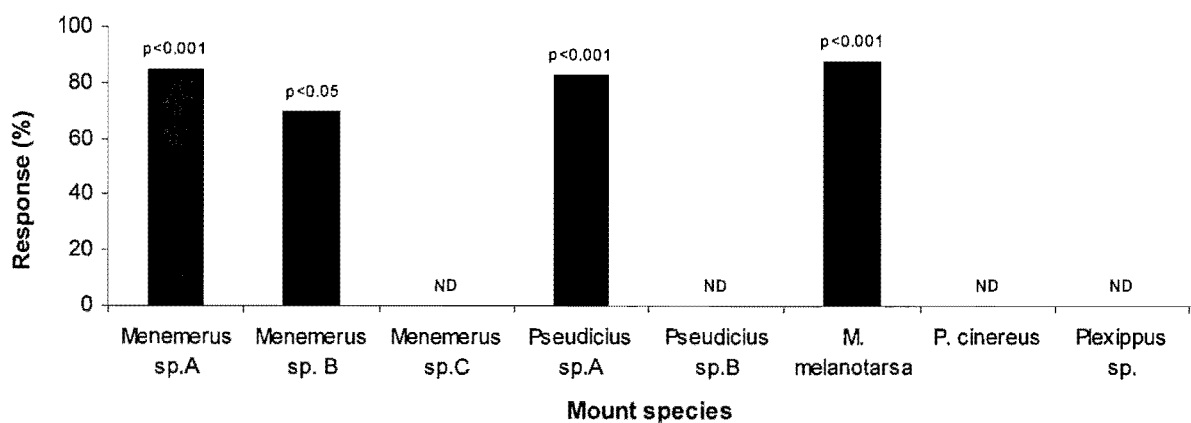
Pseudicius sp.A



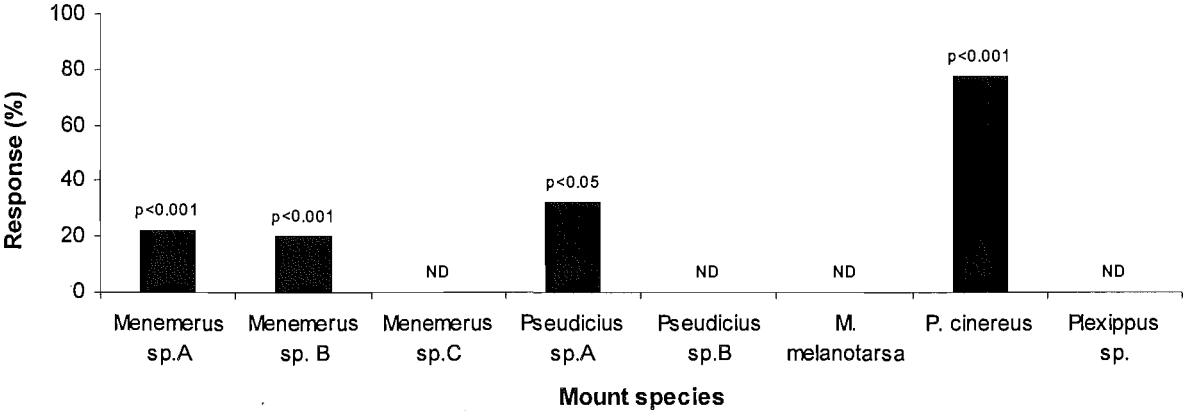
Pseudicius sp.B



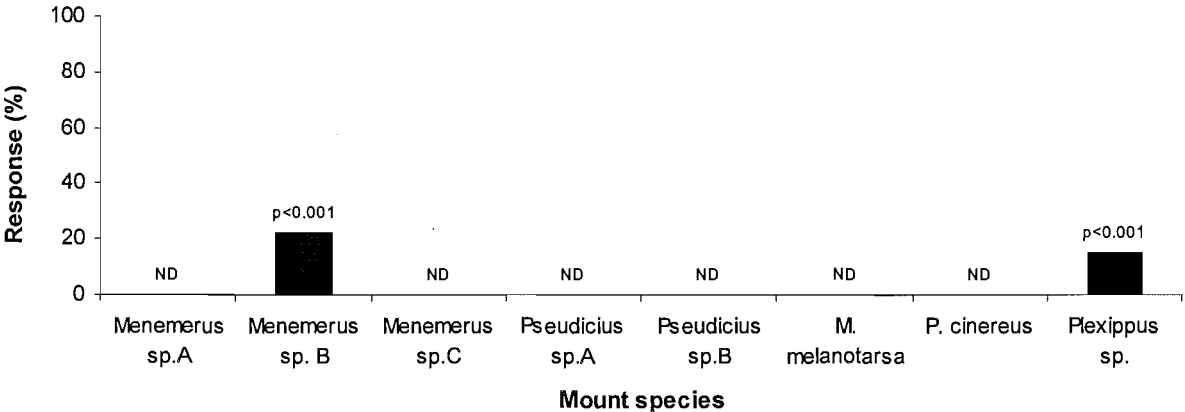
M. melanotarsa



P. cinereus



Plexippus sp.



ND= No data (not tested)

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Chapter 15

DISCUSSION

Defining Sociality

Finding a consensus on how to define terms such as term 'social', 'sociality' and 'society' has been an elusive problem, made all the more difficult by the broad diversity of animal interactions found in the natural world. The natural diversity in how animals interact in the natural world appears to be mirrored in the diversity of research priorities set by scientists, which in turn may mean that the definitions that prove useful for scientists with one set of interests will appear to trivialize the interests of other scientists. A compounding problem appears to be different views on the importance of having strict definitions for these terms at all. For example, some authors (e.g., Wilson 1975, Jackson 1979) have cautioned against defining sociality in a way that may narrow our intuitive understanding of what these words pertain to. Attempting to make strict definitions for common-language terms runs the risk of what Dennett (1996) has called 'definition mongering', a futile exercise where energy is put into word games instead of learning about the natural world. However, other authors (e.g., Shear 1970) have warned that a meaningful definition of sociality must avoid being too broad and that it is critically important for scientific rigour that we actually specify strict definitions (see Downes 1994). The ongoing dilemma seems to be whether to risk appearing unscientific by saying strict definitions are not appropriate or to go down the path of definition mongering that seems to inevitably surface when strict definitions are attempted.

A broad application of the word 'social' is suggested by having a closer look at common-language usage. The root of the word 'social' is from the Latin word 'socialis' meaning 'to associate'. Zoologically speaking, a social animal might then be envisaged as fundamentally an animal that associates with other animals. The question might then come down to whether words like 'social', 'sociality' and 'society' have any use in science, as opposed to common usage, if we keep their usage so broad.

Broad definitions are certainly nothing new in science. For example, in 1878, the French scientist Espinas affirmed that no living being is solitary, but that from the lowest to the highest each is normally immersed in some sort of social life (in Allee, 1951). Wynne-Edwards (1967) defined 'sociality' as a general phenomenon found virtually everywhere in the animal kingdom in one form or another, except in some of the most primitive groups. He envisaged a 'society' as 'an organisation capable of providing conventional competition', where this competition would in turn lead to possible rewards, including mate or territory preference. The 'rewards' he envisaged were for the group, and Wynne-Edwards' name has come to be associated closely with his discredited hypotheses about group selection. Perhaps the tainted association with group selection has been a factor in how Wynne-Edwards' ideas about sociality are now almost universally ignored. However, this might be an unfortunate consequence because his ideas on society may have considerable use when removed from the context of group selection.

At the opposite extreme, there has been a tendency to merge 'sociality' with 'eusociality'. Eusociality was originally defined by Michener (1969), and later popularized by Wilson (1971). 'Eusociality', unlike 'sociality', has had a stable, rigorous definition from the beginning: individuals of the same species that cooperate in caring for the young, show reproductive division of labour, have more or less sterile individuals working on behalf of fecund individuals, and have an overlap of at least two generations in life stages capable of contributing to colony labour. However, despite having generated interest in eusociality, Wilson (1975) retained 'sociality' as a more loosely defined general-purpose term. He acknowledged that for understanding sociality it is important to consider more than eusociality, yet his definition of 'sociality' is perhaps still too restrictive: "a group of individuals that belong to the same species and are organised in a cooperative manner". In particular, the emphasis on cooperation and the restriction to single-species groups may be problematical

Hamilton (1964) examined the genetic evolution of social behaviour in such a way that it set off a chain of research on social insects and numerous publications on altruism, haplodiploidy, and the evolution of insect sociality. Most insect sociobiologists regard Hamilton as being the first to appreciate and state clearly the full significance of Mendelian genetics and Darwin's theory of natural selection for understanding the eusocial insects. Almost all social Hymenoptera are haplodiploid. Hamilton argued that social behaviour in haplodiploid species was largely dependent on the degree of relatedness between two or more individuals. Altruistic and selfish behaviour, worker-queen conflict, ratio of investment, inclusive fitness, and other important concepts have all been related to the unique genetic asymmetries that arise from haplodiploidy in the Hymenoptera (Hamilton, 1964).

Recent studies, however, have begun to question the emphasis given to haplodiploidy when attempting to explain eusociality. It has long been acknowledged that because the diploid termites are eusocial, haplodiploidy cannot be essential for the development of eusociality (Wilson 1971, Alexander 1974), but Hamilton (1964) never actually proposed that haplodiploidy is essential. His argument was that haplodiploidy biased the cost-benefit effects of behaviour on fitness in a way that made it easier, on the whole, for eusociality to evolve. More specifically, he argued that haplodiploidy was not a 'cause' of eusociality but instead a condition that makes the conditions for kin selection easier to meet.

However, problems with the emphasis on haplodiploidy also arise when the Hymenoptera are examined closely. Genetic marker research has demonstrated that, in the colonies of the wasp *Polistes dominulus*, a haplodiploid species, unrelated individuals are often involved with helping in a colony, suggesting that kin-selection is not an adequate explanation for the altruistic acts of helping in these colonies (Queller et al, 2000). More generally, the emphasis on haplodiploidy has been criticised for focussing on the genetics of eusociality and

ignoring the ecological promoters of social evolution (Lin and Michener 1972, Alexander 1974, Evans 1977, Andersson 1984).

By trying to classify other social species using the terms derived from the literature on social insects, we risk being biased to look exclusively for characteristics and to ask questions that may not be so useful when trying to understand the societies found in other types of animals, thereby running the risk of overlooking the other group characteristics that are actually important for understanding the social species we are examining. Furthermore, if social insect characteristics are found in other societies, they may not play the same role or bear the same importance as the same characteristics in insect societies. The insect-derived classification scheme may be useful for integrating diverse comparative data, but it tends to simplify the intricacies of behaviour actually occurring among animals in the field and it may distract us from gathering the baseline descriptive data needed as a first step toward a deeper understanding of the social biology of any species (Jackson 1979, Christenson 1984).

Sociality in Vertebrate Groups

The literature on vertebrate social behaviour has, on the whole, had a perspective that differs from that in the literature on insect social behaviour. The focus in the literature on vertebrate sociality has been on group dynamics - interactions between individuals that lead to various systems of internal organisation, including dominance hierarchies, subgroups and mating associations. Vertebrate social groups (e.g. fish schools, bird flocks, ungulate groups, primate troupes) are generally seen as being based on interattraction and communication between individuals, with the function of group formation including protection from predators and efficient use of resources.

Sometimes it may seem as if insect sociality is about altruism whereas vertebrate sociality is about individualism. Vertebrate social groups tend to be viewed as the outcome of conflicting forces of cooperation and conflict among members of the group. Theories such as the

'selfish herd' model have been developed to explain why even unrelated individuals may choose to live in vertebrate groups rather than alone. Many individuals in these groups appear to behave in altruistic ways, but the vertebrate literature tends to emphasise how such behaviours may actually be viewed more appropriately as selfish (Clutton-Brock et al 1999, Blumstein 1999).

Sociality in Spiders

Spiders are notorious for being solitary, aggressive, and often cannibalistic. Social interactions do occur, but the social behaviour of spiders tends not to fit well into current evolutionary schemes. Social interactions may take the form of maternal care, interactions between recently hatched spiderlings on communal webbing and establishment of groups in adult spiders. In these cases, the spiders' activities are limited to a central location or colony.

Various authors have tried to classify the societies of the Arthropoda according to the complexity of the interactions that govern them, using definitions that introduce different restrictions for the different species studied. Societies of spiders do not lend themselves to this restrictive classification, largely because in spiders we find a continuum of intraspecific relations from solitary to social.

The study of social spiders is often, however, influenced by the large body of theory and data from the literature on social insects. Shear (1970) applied the terms 'subsocial' and 'semisocial' to spider behaviour, but these terms are confusing when used to discuss spider societies. Terms such as 'subsocial' and 'semisocial' are relevant in the insect literature in part for how they relate to eusociality. It appears that, despite the popularity these terms enjoy among social spider researchers, they may be at best inappropriate and at worst misleading when applied to social spiders.

While there are many levels of sociality among spiders, ranging from incipient aggregations to more structured communal societies, no studies of spiders have revealed the specific combinations of social characteristics seen in the eusocial insect societies. It is clear that reproductive division of labour based on morphological castes, the major feature of insect

sociality, is absent in social spiders. Instead, spiders live in societies where all members of the colony are totipotent. Furthermore the majority of spider juveniles do not require intensive adult care for survival, and co-operative behaviour that may be present appears to be based more on the sum of concurrent individual efforts on a task rather than anything like strict division of labour (Burgess 1978).

Social spiders seem to differ significantly from eusocial insects in that they do not generally rely on being in a group for survival. Social spiders can generally continue with their daily activities, such as hunting, spinning and laying eggs, without needing any assistance from other individuals. Individual eusocial insects, on the other hand, tend to survive for only a short time alone if removed from the colony (Darchen and Delange-Darchen 1986). Social spiders also do not display the colony integrity and specificity shown by many social insects. While insect colonies are usually 'closed societies', excluding all intruders, even when they are conspecifics from a different colony, all spider societies are generally 'open' (but see Rowell and Aviles 1995). Experiments on natural populations indicate that there is no distinctive colony odour and no colony exclusiveness, with all conspecific spiders experimentally introduced to a social spider group being accepted immediately as group members (Buskirk 1981).

Insect societies function especially in brood care, but spider societies appear to function more in communal web construction, resulting in a trap in which to capture prey. The silk in communal spider webs provides a special environment that assures the protection of the resident individuals and transmits information for the coordination of activities (Krafft 1982). As a consequence of grouping, inbreeding in social spiders may increase relatedness. As such, relatedness in spider societies may be a result of grouping rather than a cause of grouping.

For studying social spider groups, the approach traditionally used to study sociality in vertebrates seems to be, on the whole, more appropriate than the traditional insect-research approach. Spiders seem to live in egalitarian societies, with interactions being driven by both cooperation and conflict between individuals. Each individual apparently acts to maximise its

own benefits. In the societies of web-building spiders, webs can be conceived as not only habitations but also as prey-capture devices. A social group of spiders in a web can be envisaged as a 'foraging flock' (Uetz *et al.* 1983) and my own work suggests that, at least sometimes, group-foraging cursorial spiders may be analogous to pack-hunting social carnivores such as lions and wolves.

While social spiders do not need to be in a group to survive, an individual spider may gain benefits by grouping that outweigh the benefits gained by a solitary existence. Krafft (1970, 1982) showed that, in *Agelena consociata*, isolated individuals had a lower metabolism and developed more slowly than individuals living in a community. Juveniles of the species that were isolated as soon as they emerged from the cocoon suffered a higher mortality, slower growth, and longer duration of the first instar than young raised in groups of five individuals under conditions that were otherwise the same. This is an interesting study, although it is not entirely certain why juveniles are subject to these effects.

My own research, however, is unusual for social spider studies because the species I studied were salticids and not web-building spiders.

Mixed-species Groups

In the field, most of the East African social salticids I studied were in mixed-species groups (Chapter 2), and laboratory experiments showed that, when given the opportunity, individuals of these same species actively joined with other individuals, including individuals from different species, to form groups (Chapter 14). How we view the social behaviour of these species cannot be properly considered without taking into account the mixed-species nature of the groups. That mixed-species groups occur in this environment suggests that, when looking for the factors that influence grouping in these species, we should consider factors that apply across species and that it may be misleading to follow the tradition of giving greater (or exclusive) attention to intraspecific relationships when considering salticid sociality.

Studies concerned with inter-species interactions in mixed-species groups are now common in the literature on mammals and birds, but not so common in the literature on spiders. The lingering tradition of letting the insect literature influence how social spider groups are envisaged may be partly responsible for how little attention has been given to mixed-species groups of spiders.

In the literature on social spiders, the term ‘interattraction’ has been widely used for an inclination of individuals of the same species to join with one another. This is generally contrasted with instances of group formation brought about by individuals grouping not because they decide to join one another but because the different individuals independently end up in the same place (i.e., each is attracted to some other environmental factor instead of being attracted to each other). Interattraction of the conventional sort (i.e., between members of the same species) is in the behavioural repertoire of the East African social salticids, but individuals of most of these species also decide to join with individuals of other species, suggesting that restricting the term ‘interattraction’ to instances of same-species individuals joining is arbitrary or worse. This restriction may discourage the asking of important questions. Finding that individuals actively decide to join other individuals raises questions about adaptive significance, and considering instances of joining in which individuals belong to different species may encourage us to consider explanations that are discouraged by the tradition of emphasising single-species groups.

On the whole, the mixed-species groups that have been studied in the most detail are mammals. For example, there is strong mutual attraction between different species of tamarins (South American monkeys) (Heymann and Buchanan-Smith 2000). One of the interesting things about mixed-species groups of mammals is that there are instances in which different individuals make different joining decisions, this being something that is not generally considered when research has a strong focus on same-species groups. For example, Stensland et al (2003) studied mixed-species groups that included not only individuals that clustered as a result of mutual attraction between the participants, but also instances of individuals of a single species choosing

to join. The resulting mixed-species group formed because the presence of the attracted individual was tolerated by the individuals of the non-attracted species.

In mammal groups, hypotheses about the advantages of mixed-species groups are typically stated in terms that fall into three broad categories: foraging advantages, antipredator advantages, and social advantages.

The Cooperation-Kleptoparasitism Continuum

Traditionally, ‘cooperation’ has been considered to be a critical attribute of social spider groups, but with the meaning of ‘cooperation’ remaining unclear. In the literature on social spiders, in fact, the meaning of ‘cooperation’ seems often to overlap with that of another term, ‘tolerance’, which is also traditionally considered to be important in social spiders (Kullman 1972, Burgess 1979, Darchen and Delange-Darchen 1986, Seibt and Wickler 1988, Downes 1994). ‘Tolerance’ refers to how, in the spiders that are typically called ‘social’, there is little to no intraspecific aggression or cannibalism. Literally, ‘cooperation’ means to work (or ‘operate’) together, and it may be tempting to think that tolerance is a prerequisite for working together, but intuition here may be misleading.

The observations of prey sharing by *Portia africana* from this study may be an instructive example of how the relationship between cooperation and tolerance needs closer examination. *P. africana* juveniles live in groups, and even adults are sometimes in close proximity. Simply seeing individuals together suggests that ‘tolerance’ is an appropriate term and seeing individuals feeding on the same prey suggests the term ‘cooperative’ is applicable. However, the details of how individuals of *P. africana* interact suggest seemingly antithetical terms such as ‘conflict’, ‘competition’, and ‘aggression’. Individuals in a group of *P. africana* react to each other by dragging prey away when possible, pushing each other with their legs, by threatening each other with aggressive display, or by even by fighting. Prey sharing, when it occurs, appears to be more like a truce instead of an outcome willingly agreed to from the beginning (i.e., it appears to be an

outcome of each individual making a decision by weighing up the costs of sharing the prey against the costs of continuing to compete for exclusive access to the prey.

P. africana did not feed as a group on prey items that were especially small relative to the size of the predatory individuals. In fact, many social spiders, such as *Anelosimus studiosus* (Brach, 1977) and *Agelena consociata* (Chauvin and Denis, 1965), are known to share only large prey items. These observations suggest that the individual spider that first captures the prey must decide whether to defend the prey or to tolerate sharing, with these decisions being adaptive compromises between the advantages of defending and the costs of sharing. The costs of defending large prey may often outweigh what the individual stands to gain by refusing to share it.

In the literature on social spiders (Kullman 1968), there has been a tradition of seeing cooperation as an interaction that occurs between individuals of the same species, and an interaction that is conducted in some kind of non-aggressive way. Similar interactions between individuals belonging to different species are traditionally envisaged differently. In particular, ‘cooperation’ is the conventional term for two individuals of the same species feeding together on a single prey item and kleptoparasitism’ is the conventional term when the same behaviour is seen but with the individuals belonging to different species. Generally these cooperation-kleptoparasitism distinctions appear to be made purely on the basis of whether the species involved are the same or different, but this is too simplistic.

In the first instance, it may be misleading to distinguish between kleptoparasitism and cooperation in spiders as being two distinct categories of behaviours. It may be more realistic to envisage instances of prey sharing as varying over a continuum of levels of conflict (or the converse: different levels of willingness to share). When prey-sharing by conspecific spiders is studied in detail, evidence of conflict is common. For example, the second and third instar juveniles of *Nephila clavipes* (Hill and Christenson, 1981) may feed together in groups of up to four individuals. However, when one spiderling approaches a prey item being eaten by another,

vigorous interplay of legs is routine, and this behaviour appears aggressive. Often an intruding spiderling leaves without feeding. Even in *Anelosimus eximius*, one of the better known social web-building spiders, one female may release a prey item to lunge at and sometimes even kill another female that approaches the same prey item (Christenson, 1984).

Rather than viewing kleptoparasitism and cooperation as distinct categories of behaviour, these terms may be more useful for indicating the ends of a behavioural continuum, with 'kleptoparasitism' referring to the end of the continuum where levels of conflict are especially high, and 'cooperation' referring to the end where levels of conflict are especially low. Whether different-species examples of prey-sharing tend to be more often close to the kleptoparasitism end of the continuum, and whether same-species examples of sharing tend to be more often closer to the cooperation end, is a potentially interesting question to investigate, but we should not view the answer as a foregone conclusion.

Proximate Factors that Influence the Joining Decisions of Salticids

The basic idea of joining is that an individual animal detects cues from conspecific or non-conspecific individuals and decides whether to settle in the vicinity of the other individual (i.e., groups are not simply a consequence of individuals responding independently to the same cues from other environmental factors). Viewed this way, an animal's joining decisions are a facet of a larger strategy of choosing habitats. For a salticid, this means deciding where to live and build a nest. When making habitat choices, a salticid may consider various environmental factors, such as ambient light levels, relative humidity, and temperature (Adams, 2000), as well as objects including plant material (e.g. leaves or tree trunks) in the environment (Henschel and Lubin 1997, Lubin et al 1993). An animal may also choose a habitat on the basis of the products of other animals. For spiders, silk may often be an especially important product (Bernard and Krafft 2002, Schuck-Paim and Jimenez Alonzo 2001). Animals may also make decisions about where to settle based on the presence of particular other animals (Downes 1994).

Basically, an animal can be envisaged as assessing habitat quality when deciding whether to settle in a specific habitat, with the presence of other animals, including conspecifics, being part of what determines its perception of habitat quality. However, there appears to be a tradition of viewing the presence of conspecifics as somehow separate from habitat quality, and the effects of this more narrowly defined type of habitat quality on settling decisions have been well documented (Fretwell and Lucas 1970, Rosenzweig 1985, Ens *et al.* 1992, Sutherland 1996). The effects of cues from conspecific individuals have been studied less often (Stamps 1994, Muller *et al.* 1997). This is not surprising, as experimental studies of conspecific attraction require controlling other aspects of habitat quality, which is generally feasible only if the subjects are small, easily monitored, and easily manipulated (see Meadows and Campbell 1972, Crisp 1976, Muller *et al.* 1997).

A number of factors have been proposed as adaptive influences on an animal's joining decisions when it is specifically conspecific individuals that are being joined. For example, that an advantage of joining is increasing the chances of finding mates is a hypothesis that normally requires that the other individuals are conspecific (Shields *et al.* 1988, Stamps 1988, 1994, Mönkkönen *et al.* 1990, Forbes and Kaiser 1994). Another proposal is that an animal may use the presence of conspecifics as a cue for habitat quality in the narrow sense (i.e., quality independent of how conspecifics themselves affect quality) (Kiestler and Slatkin 1974, Alatalo *et al.* 1982, Stamps 1988), and this hypothesis is especially straight forward when the other individual is conspecific because conspecifics tend to have similar habitat requirements.

However, there are also hypotheses concerning the adaptive advantages of using other animals as habitat-choice cues that are not so strictly linked to the idea of the individuals joined being conspecific. For example, factors related prey-capture success (Rudran 1978, Munn and Terbourgh 1979), access to otherwise unavailable food (Barlow 1974, Struhsaker 1981), and decreased predation risk may often apply to mixed-species groups. Decreased predation may be especially relevant to the social salticids I studied. Reducing risk may come about through

improved detection of predators (Pulliam 1973, Struhsaker 1981, Cords 1990, Bshary and Noe 1997, Noë and Bshary 1997), decreased probability of being discovered by predators (Wolf 1985) and better active defence against a predator's attacks (Chapman and Chapman 1996). All of these hypotheses can be formulated as hypotheses concerning the role of other animals as habitat-choice cues, with necessarily stipulating that the other animals are conspecific.

My research has revealed considerable variation in the types of groups formed by different salticid species. While the multi-species groups were common, the 'Nuns' and *Parajotus cinereus* were almost always found in single-species groups, with the common Nun group being a pair of conspecific adult females. For the Nuns, it appears to be specifically the presence of one conspecific female that serves as a joining cue. For *P. cinereus*, the joining cue seems to be simply any other conspecific individuals, and *P. cinereus* groups were usually much larger than the Nun pairings and contained males and juveniles as well as females.

Variation in joining decisions is also evident for the salticids that form mixed-species groups, and again the variation can be used to formulate hypotheses about habitat-choice cues. For example, *Myrmarachne melanotarsa* seems to use the presence of conspecifics and various other salticids as cues for joining, whereas the presence of *M. melanotarsa* does not appear to be a cue for joining for some of the other salticids with which *M. melanotarsa* joins.

My research has shown that grouping with other individuals may entail a variety of costs and benefits for the individual salticid. Different salticid species tend to make different joining decisions, and some salticids choose to join individuals that are not conspecific. Protection from predators appears to be an especially important benefit of joining.

It is important to understand that joining involves more than one individual, and that groups may be formed by a mixture of individuals that make active decisions to join and others that only tolerate joiners rather than actively choosing to join. There are also likely to be 'leavers' (i.e., individuals that leave when other individuals join them), and yet other individuals who may control group membership by selectively driving away particular types of joiners. Any

two individuals in a group may be subject to different cost-benefit effects of joining and it may be misleading to use the term 'interattraction' with its implication that every individual in a group is there with similar, if not identical, motivation.

The true complexity of the interactions and different decisions by individuals in a group may sometimes defy simple explanation, and we may often use oversimplifying expressions as a shorthand or convenience. This is all right so long as we stay on guard against shorthand expressions masquerading as explanations. However, even the shorthand should perhaps be chosen carefully.

One of the main impressions that developed in the course of my research is that the prevalent shorthand expressions applied to social spiders (e.g., 'cooperation', 'tolerance' and 'interattraction') may be seriously misleading. Perhaps any one model or any one classification scheme for social spiders will never be fully satisfactory, and it may be more instructive to focus research on the balance of cost and benefit behind the decisions being made by individual animals.

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